Early Cretaceous macrofloras of Western Australia

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Abstract - Western Australian, Lower Cretaceous, macrofloras from the Broome Sandstone and Callawa Formation (Canning Basin), Nanutarra Formation and Birdrong Sandstone (Carnarvon Basin), Cronin Sandstone (Officer Basin), and Leederville and Bullsbrook Formations (Perth Basin) incorporate a range of lycophytes, ferns, pteridosperms, bennettitaleans, and conifers. The new monotypic genus Roebuckia is established for spatulate fern fronds (R. spatulata) of possible vittariacean alliance. Other newly established species include Phyllopteroides westralensis, Elatocladus ginginensis, and Carpolitlies bullsbrookensis. Although the Western Australian fossil suites reveal some specific differences from other Australian late Mesozoic assemblages, several shared index taxa and the high proportion of bennettitaleans support correlation with the Victorian Neocomian Ptilophyllum-Pachypteris austropapillosa Zone (Zone B). Some Western Australian taxa are shared with Indian assemblages but fewer similarities exist with other Gondwanan Early Cretaceous floras. The representation of several hydrophilous fern, lycophyte, and pteridosperm groups together with growth indices from fossil woods implies a seasonal humid mesothermal climate for the Western Australian cratonic margin during the Neocomian-Barremian. Minor differences between the Western Australian assemblages are attributable to local depositional and preservational factors.

INTRODUCTION

This paper reviews all Western Australian Cretaceous plant fossils held in the collections of the Western Australian Museum and the Department of Geology and Geophysics of the University of Western Australia together with limited material held in the Australian Museum, Sydney. As all specimens lack preserved organic matter, descriptions are based on gross morphology, ornamentation, and venation patterns. This procedure necessarily places limitations on the degree of discrimination between some taxa. However, the scarcity of previous studies on the Western Australian fossil floras invites this systematic appraisal in order to fill some major gaps in the knowledge of Australia's Cretaceous phytogeography.

The relative tectonic stability and deepweathering associated with much of the central and western part of the Australian continent since the mid-Mesozoic has removed from outcrops most of the organic material required for palynological studies. Apart from scarce vertebrate trackways (Colbert and Merrilees 1967; Long 1990), plant macrofossils are virtually the only fossil remains available in outcrop to date and palaeoenvironmentally categorize Western Australian Cretaceous terrestrial strata. No studies dealing with stratigraphic and petroleum exploration drilling have reported significant

assemblages of plant macrofossils from subsurface Cretaceous strata in Western Australia. Retallack (1977, 1980) and McLoughlin (1993) have illustrated differences in palaeosol development and the composition of plant fossil assemblages in Australian Permian and Triassic strata according to variations in local and regional depositional settings. Such sedimentological and taphonomic controls also apply to the Cretaceous assemblages offering an important tool for detailed interpretation of non-marine sedimentary facies. Additionally, permineralized, mollusc-bored, driftwood preserved in Lower Cretaceous marine sediments has aided the definition of sequence stratigraphic boundaries and systems tracts et al. 1994). Palaeobotanical (McLoughlin investigations of the diversity of plant groups together with anatomical indices such as growth ring variation are also useful for the categorization of palaeoclimates and the identification of major food sources available to the large Cretaceous herbivorous dinosaurs.

PREVIOUS STUDIES

Douglas (1969, 1973), Drinnan and Chambers (1986) and McLoughlin *et al.* (1995) have provided the most detailed studies of Australian Cretaceous fossil plants dealing with macrofloras from the Gippsland, Otway and Eromanga Basins. Other



Figure 1 Map of Western Australia showing Phanerozoic sedimentary basins and principal Cretaceous plant macrofossil localities (solid squares).

significant contributions include those of Seward (1904), Chapman (1908, 1909, 1914), Walkom (1918, 1919a), Medwell (1954a,b), Glaessner and Rao (1955), and Dettmann et al. (1992). Although several stratigraphic papers have provided lists of fossil plants recovered from Western Australian Cretaceous strata (e.g., Brunnschweiler 1960; Cox 1961; Playford et al. 1976) many of these identifications are not supported by illustrations or descriptions and are commonly erroneous. A small assemblage described and illustrated by Walkom (1944) from strata underlying the Molecap Greensand near Gingin is redescribed herein. White (1961a) briefly described and illustrated plant remains recovered from the Canning Basin by Australian Bureau of Mineral Resources regional geological surveys. McLoughlin and Guppy (1993), and McLoughlin and Hill (in press) provided preliminary revised lists of Western Australian Cretaceous plant fossils from several sedimentary basins and briefly discussed some palaeoclimatic implications of the floras.

McLoughlin *et al.* (1994) detailed the anatomical character and palaeoenvironmental significance of silicified and phosphatized woods from the Birdrong Sandstone, Carnarvon Basin and Backhouse *et al.* (1995) described lignitized but anatomically similar woods from the Barremian to earliest Aptian Nakina Formation of the Collie Basin. The Cretaceous palaeobotanical literature from other Gondwanan continents (especially India and South America) is extensive. Therefore, synonymy lists provided here deal only with previously figured or described Western Australian fossil plants.

CRETACEOUS STRATIGRAPHY

Western Australian Cretaceous plant macrofossils have been recovered from the Perth, Carnarvon, Canning, and Officer Basins (Figure 1). Plant remains are best represented in Early Cretaceous non-marine strata (Figure 2). Due to a dearth of palynological studies and the absence of

marine invertebrate biostratigraphic indices, the ages of many of these rock units are only broadly constrained. Furthermore, lack of continuous outcrops in many areas hinders the mapping and lithological correlation of plant-bearing strata and has led to uncertainties over the application of lithostratigraphic names. For example, Playford *et al.* (1976) and Skwarko (1990) assigned Walkom's (1944) Gingin fossil assemblage to the Yarragadee Formation (Middle Jurassic to Tithonian). However, Feldtman (1963) reported that the plantbearing horizons occurred within the Strathalbyn Beds, a term which Playford *et al.* (1976) regarded as synonymous with the Leederville Formation. Wilde and Low (1978) also mapped outcrops in the vicinity of Walkom's plant beds (Cheriton Creek) as part of the Leederville Formation. On the basis of lithology and stratigraphic position, the fossils are here regarded as belonging to the marine to continental Leederville Formation (Hauterivian–



Figure 2 Stratigraphic correlation of Lower Cretaceous rock units in the Perth, Carnarvon, and Canning Basins, Western Australia (after Cockbain 1990; Hocking 1990; Middleton 1990) showing the distribution of plant macrofossil assemblages.

Barremian): Figure 2. The Bullsbrook Formation, exposed 2 km east of Bullsbrook, is a fully continental lateral equivalent of the Leederville Formation (Figure 2).

The Neocomian-?Aptian shallow marine to paralic Birdrong Sandstone is chiefly exposed along the Murchison River near Kalbarri, on the flanks of the Kennedy Ranges, and in the Giralia Anticline within the Carnarvon Basin (Hocking et al. 1987; McLoughlin et al. 1994). The upper part of this unit is typically rich in fragmentary permineralized gymnosperm wood showing evidence of intensive molluscan borings. Other Cretaceous marine units in the Carnarvon Basin contain sparse fossil woods, and leaf impressions occur within the paralic Nanutarra Formation near the Ashburton River (Figure 1). Lignified wood is also locally preserved in the Lower Cretaceous Nakina Formation, Collie Basin, in the state's southwest (Backhouse et al. 1995).

The Broome Sandstone of the northern Canning Basin was deposited within deltaic to shallow marine environments whereas the laterally equivalent Callawa Formation in the basin's southwest is fluvial in origin (Towner and Gibson 1983). The coeval Cronin Sandstone, outcropping in the northwestern part of the contiguous Officer Basin (Figures 1,2) was also laid down in fluvial environments (Towner and Gibson 1983). These plant-bearing units have been regarded as Late Jurassic to Early Cretaceous or even fully Jurassic on the basis of previous phytostratigraphic interpretations (Middleton 1990). However, a Neocomian-Barremian age for the plant-bearing portions of these units is proposed herein based on revised fossil identifications.

MATERIAL AND METHODS

The majority of material described and figured in this study is held in the collections of the Western Australian Museum (specimens prefixed WAM) and the Department of Geology and Geophysics, University of Western Australia (specimens prefixed UWA). Counterparts of some of Walkom's (1944) specimens are lodged with the Australian Museum in Sydney (specimens prefixed AMF). The Commonwealth Palaeontological Collection housed by the Australian Geological Survey Organisation, Canberra, contains limited Canning and Officer Basin material from regional geological surveys of the 1950s and 60s and has been illustrated by White (1961a). The latter material was not re-examined during this study but in most cases White's (1961a) illustrations are adequate for identification purposes and her studied specimens are systematically discussed herein.

All descriptions are based on impression fossils

preserved in ferruginous shale and mediumgrained quartzose sandstone apart from some seeds, megaspores, and axes which are preserved as natural clay or sandstone casts. Organic material was not preserved on any fossils but in some cases latex and silicone casts yielded morphological details not clearly evident on negative impressions. All specimens were illustrated under strong unilateral light directed from the upper left unless otherwise stated.

Fossil localities are as follows:

- Broome Sandstone Gantheaume Point, Broome (material collected by W.H. Butler, A. Dawson, I. and T. Foulkes, J. Long, D. and M. Merrilees, J. Pas, G. Zeck); Quandong Beach, 10 km north of Broome lighthouse (material collected by 1.M. Doust).
- Nanutarra Formation Cited as "6.5 km north of Globe Hill, Ashburton River" on specimen labels (material collected by D.W. McLeod). This is probably the plant fossil locality 2.5 km north of the junction of Jubricoo Creek and Ashburton River, 8 km west of Nanutarra indicated by van de Graaf *et al.* (1980).
- Birdrong Sandstone Near Toolonga Hill (114°16'6"E 27°34'3"S), Murchison House Station, 10 km northeast of Kalbarri (material collected by S. McLoughlin); 1 km northwest of Black Dam (114°10'9"E 23°6'3"S), Cardabia Station, 35 km east of Coral Bay (material collected by D.W. Haig, R. Howe, G. Ellis, S. McLoughlin).
- Leederville Formation Cheriton Creek, about 500 m east of MacIntyre Gully, 2.5 km north of Gingin (material collected by E. de C. Clarke).
- Bullsbrook Formation 2.5 km northeast of Bullsbrook Hotel (material collected by A. Page).

SYSTEMATIC PALAEOBOTANY

Division Lycophyta

Class Lycopsida

Order Isoetales

Family Isoetaceae

Genus Isoetites Münster, 1842

Type species

Isoetites crociformis Münster, 1842; Jurassic; Daiting near Manheim, Germany.

Isoetites elegans Walkom, 1944 Figures 3A, C-F

1944 *Isoetites elegans* Walkom; p. 202; plate 1, figs 1– 5.

1993 Isoetites elegans; McLoughlin and Guppy; p. 14; figure 12.

Holotype

UWA16687; Leederville Formation (Neocomian-Barremian), Perth Basin, Western Australia (Walkom 1944).

Material

UWA16682, UWA16683 (principal sporangiabearing specimen), UWA16684, UWA16685, UWA16687 (principal foliage-bearing specimen), UWA16690, UWA16703, UWA16711. Counterparts of some specimens are held in the Australian Museum (AMF39815: see White 1986, figure 260).

Distribution

Leederville Formation (Neocomian–Barremian), Perth Basin, Western Australia. Previous assignation of these specimens to the Jurassic (Walkom 1944; Ash and Pigg 1991) is now deemed erroneous.

Description

Numerous (>30) radiating linear leaves, reaching at least 10 cm long, 5 mm wide, bases not preserved, apices pointed, margins entire (Figure 3A). Longitudinal striae evident on some leaves but venation otherwise indistinct. Associated megasporophylls on type locality slabs bear clusters of numerous (>30) trilete megaspores. Megasporophylls identical to sterile leaves, showing no expansion around sporangia. Megasporangia reach 10 mm long, 2.5 mm wide (Figure 3C). Megaspores 0.5 mm in diameter, circular in polar compression, laesurae prominent; contact surfaces extending almost to the equator, laevigate; distal surface reticulate (moulds coarsely granulate: Figure 3D). Associated microsporophylls bear elliptical microsporangia, 10 mm long, 3 mm wide, consisting of densely matted casts of ill-defined microspores (Figures 3E,F).

Comments

Although the earliest records of *Isoetites* are from the Upper Triassic (Bock 1962), they underwent a phase of global diversification during the Early Cretaceous (Pigg 1992). Ash and Pigg (1991) listed the fossil species previously assigned to *Isoetites* Münster 1842 and *Isoëtcs* Linnaeus 1753. All examples essentially consist of linear leaves or sporophylls either in isolation or attached in rosettes to short cylindrical or spherical corms. Other species can be distinguished from *I. elegans* by possession of serrate leaf margins (*Isoetites serratus* Brown, 1939, *Isoctites serratifolius* Bose and Roy, 1964), air channels within the leaves (*Isoetites horridus* (Dawson) Brown, 1939), the details of megaspores and cuticle (*Isoetites clioffati* Saporta, 1894, *Isoetes reticulata* Hill, 1987), leaf proportions (*Isoetites granineoides* Bock, 1962, *Isoetites rolandii* Ash and Pigg, 1991), and corm dimensions (*Isoetites crociformis* Münster, 1842, *Isoetites circularis* (Emmons) Brown, 1958).

Isoetes janaianus Banerji, 1989 from the Middle to Upper Jurassic of India has similar leaves and sporangia to *I. elegans* but is characterized by a 5lobed rhizomorph whereas corms are not yet available for the latter species. *Isoetites bulbiformis* Drinnan and Chambers, 1986 from the Victorian Lower Cretaceous, distinguished by its smaller size and expanded leaf tips, may represent gymnospermous remains. The Indian Lower Cretaceous *Isoetites indicus* Bose and Roy, 1964, although represented only by sporophyll bases, is characterized by its smaller but more numerous megaspores in each sporangia (Bose and Banerji 1984).

Genus Nathorstianella Glaessner and Rao, 1955

Type species

Nathorstianella babbagensis (Woodward) Glaessner and Rao, 1955; Lower Cretaceous; Mt Babbage, South Australia.

Nathorstianella babbagensis (Woodward) Glaessner and Rao, 1955 Figure 3B

cf. 1961 "fragment of stem" White; p. 304; plate 6, figure 3. [1961a].

Holotype

F15070 (Adelaide University Geology Department); Algebuckina Sandstone (Neocomian); Mt Babbage, South Australia (Glaessner and Rao 1955).

Material

WAM P.88.2, WAM P.96.12.

Distribution

Algebuckina Sandstone (Berriasian-early Valanginian), Eromanga Basin, South Australia (Dettmann *et al.* 1992); Broome Sandstone (Neocomian-Barremian), Canning Basin, Western Australia (this study).

Description

Fragmentary casts of cylindrical axes (14–17 mm wide, 24–35 mm long) bearing numerous spirally arranged leaf or root scars (Figure 3B). Scars diminutive (0.5 mm wide, 0.25 mm high), c. 0.5–1



mm apart, arranged in flat $(70^{\circ}-75^{\circ})$ right-handed and steep (50°) left-handed spirals (measured with respect to axial orientation). Axes show broad transverse ridges or undulations corresponding to growth increments. Attached roots unavailable. Leaves unavailable on curated specimens.

Comments

Glaessner and Rao (1955) suggested a possible relationship between leafless Nathorstianella corms and foliage assigned to Isoetites elegans. Leaves 4 mm wide, 60 mm long and similar to I. elegans, but lacking sporangia, were observed attached to N. babbagensis axes in outcrops of the Broome Sandstone at Gantheaume Point near Broome during this study. The specimens are preserved in rock slabs too large to be collected or extracted without risking damage to the fossils. It seems likely that I. elegans leaves and N. babbagensis belonged to the same plant although formal synonymy should wait until fertile material is found attached to the latter. The occurrence of N. babbageusis in sandy deltaic sediments of the Broome Sandstone suggests that this plant preferred coastal habitats similar to those occupied by related herbaceous to arborescent Triassic pleuromeian lycophytes (Retallack 1977; Karrfalt 1986).

Division Pteridophyta Class Filicopsida

Order Filicales

Family Dipteridaceae

Genus Hausmanuia Dunker, 1846

Type species

Hausmannia dichotoma Dunker, 1846; Jurassic; near Buckenburg, Bavaria.

Hausmannia sp. Figures 4A,C

- 1961 *Hausmannia* sp.; White; p. 306; plate 8, figure 4. [1961a].
- 1993 *Hausmanuia* sp.; McLoughlin and Guppy; p. 14; figure 7.

Material

WAM P.65.42, WAM P.88.13, WAM P.89.166, WAM P.89.181, WAM P.96.9.

Distribution

Broome Sandstone (Neocomian-Barremian), Canning Basin; Lees Sandstone (Neocomian?), Carpentaria Basin, Northern Territory (White 1961b; Dettmann *et al.* 1992).

Description

Frond flabellate, up to 42 mm long and 47 mm wide; base cuneate, tapering to long petiole (Figure 4C); apex rounded, undulate, or broadly dentate. Single vein enters base of frond from petiole, bifurcates up to six times producing a radiating array of dominant veins; each ultimate dominant vein enters base of a marginal tooth (Figure 4A). Up to five orders of closely anastomosing subsidiary veins subdivide lamina between dominant veins into a meshwork of <0.25 mm² aureoles. Petiole 1 mm wide, >6.5 cm long. Sporangia not evident.

Comments

Hausmannia has affinities with reticulate-veined pinnatifid dipteridacean fronds such as Goeppertella Oishi and Yamashita emend. Arrondo and Petriella, 1982, Dictyophyllum Lindley and Hutton, 1834, Thaumatopteris Goeppert, 1841, and Clathropteris Brongniart, 1828 (Herbst, 1975). Hausmannia had a cosmopolitan distribution during the Jurassic and Cretaceous (Corsin and Waterlot 1979) with several species known from gondwanan continents, although some are based on scanty material.

Hausmannia papilio Feruglio emend. Herbst 1960 fronds from the Early Cretaceous of Argentina are most closely comparable to the Western Australian specimens although examples of the former do not show long petioles and are more circular with slightly auriculate bases (Herbst 1960). Hausmannia pachydernia Sukh-Dev 1972b and specimens assigned to Hausmannia crenata (Nathorst) Möller from India (Bose and Sah 1968) can be distinguished from the Western Australian form by their undulate margins and coarsely reticulate venation. The Indian H. crookshauki Shah and Singh, 1964 differs by its apically cleft lamina.

Of the previously described Australian

Figure 3 A *lsoetites elegans* Walkom 1944; Rosette of linear univeined leaves; UWA16687; Leederville Formation; x 0.8; B, *Nathorstianella babbagensis* (Woodward) Glaessner and Rao, 1955; Corm impression with spirally arranged leaf/root scars; WAM P.88.2; Broome Sandstone; x 3; C, Megasporangia of *lsoetites elegans* Walkom, 1944; UWA16683; Leederville Formation; x 8; D, Scanning electron micrograph of *lsoetites elegans* Walkom, 1944 megaspores; AMF39815; Leederville Formation; x 100; E, Microsporangia (Mi) and megasporangia (Me) of *lsoetites elegans* Walkom, 1944; UWA16683; Leederville Formation; x 4; F, Scanning electron micrograph of surface of *lsoetites elegans* Walkom, 1944 microsporangium showing ill-defined microspore outlines; AMF39815; Leederville Formation; x 1000.



Hausmannia species, Herbst (1979) considered that only H. wilkinsii Walkom, 1928, H. sp. cf. H. defarrariisii Feruglio, 1937, and H. bulbaformis Douglas, 1973 were distinguishable. Hausmannia wilkinsii and H. bulbaformis are both differentiated from the Western Australian form by their strongly dissected lamina (Walkom 1928; Douglas 1973). Hausmannia sp. cf. H. defarrariisii from the Middle Jurassic Walloon Coal Measures (Herbst 1979; McLoughlin and Drinnan 1995) differs by its pronounced apical lamina incision and auriculate base with respect to both Northern Territory fronds illustrated by White (1961b, 1966) and the forms from the Broome Sandstone. It is likely that both the Northern Territory and Western Australian Early Cretaceous forms are conspecific.

Order Osmundales

Family Osmundaceae

Genus Cladophlebis Brongniart, 1849

Type species

Cladophlebis albertsii (Dunker) Brongniart, 1849; ?Jurassic; Germany.

Cladophlebis sp. cf. C. oblonga Halle, 1913 Figures 4B,D,G

- 1961 Cladophlebis australis (Morris); White; p. 304; plate 7, figures 1, 6. [1961a].
- 1993 *Cladophlebis* sp. cf. *C. oblonga*; McLoughlin and Guppy; figure 2.

Material

WAM P.64.5, WAM P.65.40, WAM P.88.9, WAM P.88.10, WAM P.88.12.

Distribution

Broome Sandstone, Canning Basin; Bullsbrook Formation, Perth Basin; Algebuckina Sandstone, South Australia (all Lower Cretaceous).

Description

Fronds pinnate or bipinnate (imparipinnate). Rachis prominent, striate, <1.5 mm wide, gently tapering distally. Pinnules alternate, oblong, up to 6 mm wide, 18 mm long; apex rounded to obtusely pointed, margin entire, basiscopic margin straight or convex, acroscopic margin straight (Figures 4B,D). Adjacent pinnule bases contiguous. Pinnules arise at c. 50° from rachilla. Pinnules have alethopteroid venation; veins depart pinnule midrib at 50°–60°, bifurcate once or twice, pass straight to margin, no anastomoses (Figure 4G). Pinnule midribs evanescent c. 3 mm before apex.

Comments

Cladophlebis foliage is abundant and widespread in Permian to Cainozoic strata throughout the world. Many species referred to this genus have been assigned to the Osmundaceae based on the possession of osmundaceous sporangia and spores association or by with permineralized osmundaceous axes. Specimens lacking attached axial or fertile remains are assigned to a large array of form species based on frond and pinnule shape and venation patterns. The variation of pinnule shapes evident on different parts of some extant fern fronds suggests that description of inadequate material may have led to a proliferation of names for Cladophlebis species.

Australian cladophleboid fronds from a wide range of localities and ages have been commonly assigned to Cladophlebis australis (Morris) Seward, 1904, a species originally erected for Triassic fronds from Tasmania (Morris 1845). The variation in Australian C. australis pinnule shapes appears to be roughly equivalent to the range evident between the many South American species (Herbst 1971). Morris's (1845) original illustrations of C. australis show slender tapering falcate pinnules quite different from the Western Australian form described here. The studied specimens are compared with C. oblonga Halle, 1913 based on their relatively oblong pinnules with rounded or weakly pointed apices although some Antarctic and South American examples of this species have slightly shorter and more falcate pinnules than the Western Australian forms (Halle 1913; Herbst 1971; Arrondo and Petriella 1980). Though poorly preserved and slightly smaller, White's (1961a) oblong Cladophlebis australis pinnae from the Callawa Formation appear to be conspecific with the Broome and Bullsbrook fronds as are the South Australian specimens of Glaessner and Rao (1955).

Figure 4 A, Hausmannia sp.; WAM P.88.13; Broome Sandstone; x 2; B, Cladophlebis cf. oblonga Halle, 1913; UWA10465A; Bullsbrook Formation; x 2; C, Hausmannia sp.; Two fragmentary fronds with long slender rachises; WAM P.89.181; Broome Sandstone; x 1; D, Cladophlebis cf. oblonga Halle, 1913; Pinna with preserved apex; WAM P.88.12; Broome Sandstone; x 1.5; E,F,H, Isolated pinnules of Phyllopteroides westralensis sp. nov.; (E) UWA10473, (F) UWA10473, (H) UWA10467C; Bullsbrook Formation; all x 3; G, Cladophlebis cf. oblonga Halle, 1913 showing details of venation; WAM P.88.9; Broome Sandstone; x 2; I, Microphyllopteris gleiclenioides (Oldham and Morris) Walkom 1919a; Enlargement showing details of pinnae; WAM P.88.1; Broome Sandstone; x 3.

Walkom's (1919a) Early Cretaceous *C. australis* specimens from Queensland are also comparable in terms of pinnule shape but appear to have more prominent, but less divided, secondary veins. The Western Australian fronds have similarly proportioned pinnules and venation patterns to *Cladophlebis* sp. cf. *C. oblonga* Halle, 1913 of Drinnan and Chambers (1986) although the Victorian examples have more sharply acute apices.

The oblong shape and generally rounded pinnule apices of the Western Australian specimens distinguish them from many of the Indian Mesozoic *Cladophlebis* species which typically have either shorter elliptical or more narrow and elongate (lanceolate to falcate) pinnules often with acutely pointed apices (Bose and Sah 1968; Sukh-Dev 1972a; Zeba-Bano 1980; Roy 1968; Bose and Banerji 1984; Kasat 1970).

Herbst (1971) reviewed South American Mesozoic fronds assigned to 17 *Cladophlebis* species. Of these, *C. denticulata* Brongniart, 1828 and *C. patagouica* Frenguelli, 1947 have similarly sized oblong pinnules to the Western Australian specimens but are distinguished by their prominently pointed acute apices (Baldoni 1980a; Longobucco *et al.* 1985). The Western Australian specimens compare favourably to Archangelsky's (1964b) *Cladophlebis* sp., *C. oblonga* Halle, 1913, *C. pintadeusis* Herbst, 1966, and *C. haiburnensis* var *rectimarginata* Herbst, 1966 and it appears that few individual features enable consistent differentiation of these species in the absence of fertile or cuticular material.

South African Early Cretaceous *Cladophlebis bezuidenhoutensis* Gianniny and Wiens and *C. dunbrodiensis* Gianniny and Wiens (in Anderson and Anderson, 1985) fronds clearly differ from the Western Australian form by their undulate pinnule margins. Other South African species differ by their smaller, more elongate, contracted or falcate pinnules (Anderson and Anderson 1985).

Genus Phyllopteroides Medwell, 1954b

Type species

Phyllopteroides dentata Medwell, 1954b; Early Cretaceous; Killara, Otway Basin, Victoria.

Phyllopteroides westralensis sp. nov. Figures 4E,F,H; 5A

- 1961 Linguifolium denneadi Jones and de Jersey; White; p. 302; plate 5, figure 3. [1961a].
- 1993 *Phyllopteroides lanceolata;* McLoughlin and Guppy; figures 4, 11.

Holotype

UWA10473C (Figure 5A); Bullsbrook Formation

(Neocomian-Barremian); Bullsbrook, Perth Basin, Western Australia.

Etymology

Signifying the Western Australian distribution of the species.

Material

WAM P.96.11. UWA10461D, UWA10462A, UWA10464A, UWA10467C, UWA10470A-B, UWA10472A, UWA10473B-D, E-F, UWA10474C.

Distribution

Broome Sandstone, Canning Basin; Bullsbrook Formation, Perth Basin; Cronin Sandstone, Officer Basin (all Neocomian-Barremian).

Diagnosis

Fronds imparipinnate; pinnules narrowly elliptical to lanceolate, base tapering acute with short petiolule, apex rounded, margin entire or gently undulate; secondary veins once or twice dichotomous, 15–20 veins per cm, intersecting margin at 20°–40°.

Description

Fronds pinnate (imparipinnate). Rachis slender (<2 mm) wide. Pinnules narrowly elliptical to lanceolate, reaching 10 mm wide, 40 mm long, inserted alternately on rachis at c. 40° (Figure 5A). Base tapering acute, joined to rachis by short (<2 mm petiole), apex rounded, margin entire or gently undulate. Pinnules show weakly defined evanescent midrib. Secondary veins once or twice dichotomous, arch gently from indistinct midvein to intersect margin at 20°-40°, 15–20 veins per cm; no anastomoses (Figures 4E,F,H).

Comments

Cantrill and Webb (1987) re-evaluated the genus Phyllopteroides and indicated its likely affinity to the Osmundaceae based on the association of sterile P. dentata fronds with osmundaceous sporangiate remains (Caecumen expansa Cantrill and Webb, 1987). Five species (viz., P. dentata Medwell, 1954b, P. lanceolata (Walkom) Medwell, 1954b, P. serrata Cantrill and Webb, 1987, P. laevis Cantrill and Webb, 1987, and P. macchymoutae McLoughlin, Drinnan and Rozefelds, 1995) have been described from Australia. The entire-margined lanceolate Western Australian leaves compare most closely with P. lauceolata identified from Albian strata of central Queensland (Walkom 1919a). However, P. westralensis sp. nov. differs by its consistently entire pinnule margins, substantially lesser venation angle, and generally lesser vein densities. Phyllopteroides deutata, P. serrata and P. macclymoutae can be distinguished by their strongly

dentate or serrate margins. *Phyllopteroides laevis* leaflets may also have entire margins, however, they differ from *P. lanceolata* by their more broadly elliptical shape. White's (1961a) *Linguifolium denmeadi* from the Cronin Sandstone, Officer Basin, is here regarded as a detached *P. westralensis* pinnule.

Cantrill and Webb (1987) suggested that the successive stratigraphic ranges of P. laevis, P. serrata, and P. deutata in Victoria represented elements of an evolutionary lineage. They also suggested that the Queensland P. lanceolata arose from the same Neocomian-Aptian stock but evolved independently of the Albian P. dentata of Victoria. The Neocomian-Barremian P. westralensis may represent a separate lineage derived from entire-margined P. laevis stock which became restricted to the lowlands of the continent's western margin. Few fossil fronds outside Australia are comparable with P. westralensis although Thiunfeldia chunakhalensis Sah and Sukh Dev, 1958 may be referable to Phyllopteroides based on its P. laevis-like pinnules.

Order Gleicheniales

Family Gleicheniaceae

Genus Microphyllopteris Arber, 1917

Type species

Microphyllopteris pectinata (Hector) Arber, 1917; Lower Jurassic; Mataura Falls, New Zealand.

Microphyllopteris gleichenioides (Oldham and Morris) Walkom, 1919a Figures 41; 5B

1993 Microphyllopteris gleichenoides; McLoughlin and Guppy; figures 5, 6.

Lectotype

No. 4444 (Geological Survey of India, Calcutta); Rajmahal Series (?Lower Cretaceous), Rajmahal Hills, India. Selected by Bose and Sah (1968).

Material

WAM P.88.1.

Distribution

Broome Sandstone (Neocomian-Barremian), Canning Basin; Dalrymple Sandstone (Upper Jurassic), Laura Basin, Queensland (Walkom 1928); Burrum Coal Measures (Albian), Maryborough Basin, Queensland (Walkom 1919a); Rajmahal Series and equivalents (Lower Cretaceous) of Peninsula India (Seward and Sahni 1920; Bose and Sah 1968).

Description

Frond at least bipinnate (Figure 5B). Rachis slender (<2 mm wide). Pinnae linear, opposite to subopposite, arched distally, up to 2.5 mm wide, 30 mm long, inserted on rachis at 70°–90°. Pinnules minute (1×1 mm), showing full basal attachment, semicircular, alternate, apices rounded (Figure 4I). No sporangia evident.

Comments

Arber (1917) established Microphyllopteris for fronds resembling extant Gleichenia ferns but lacking definitive evidence for a relationship to that genus. However, many workers have continued to assign such fronds to Gleichenites Goeppert, 1836 or Gleichenia Smith, 1793 even in the absence of fertile material. Microphyllopteris gleichenioides (Oldham and Morris) Walkom 1919a and comparable forms have been reported from Upper Jurassic to mid-Cretaceous strata in Queensland (Walkom 1919a, 1928; McLoughlin et al. 1995). Gleichenites nanopinnatus (Douglas) Drinnan and Chambers 1986 from the Lower Cretaceous of Victoria has larger and more dissected pinnules than M. gleichenioides.

Gleichenites sp. of Arrondo and Petriella (1980) from the Argentinian Jurassic is a much larger frond than *M. gleichenioides* but has similar pinnules and may be closely related to the Australian species. *Gleichenites sanmartinii* Halle emend. Herbst 1962a and *G. vegagrandis* Herbst, 1962a from the Cretaceous of Argentina and Antarctica also have similar diminutive semicircular pinnules although these are slightly inclined distally (Herbst 1962a, b).

Some Indian examples of 'Gleichenites gleichenoides' and Microphyllopteris sp. illustrated by Sah (1965) and Bose and Sah (1968) differ slightly from the Australian *M. gleichenioides* in having pinnules which are strongly deflected towards the pinna apex (insertion angle about 60°).

Order ?Pteridales

Family ?Vittariaceae

Roebuckia gen. nov.

Type species

Roebuckia spatulata sp. nov.; Broome Sandstone (Neocomian-Barremian); Gantheaume Point, Broome, Canning Basin, Western Australia.

Diagnosis and discussion

See under Roebuckia spatulata below.

Distribution

Known only from the type formation.



Roebuckia spatulata sp. nov. Figures 5E,F

1993 Indeterminate spatulate frond; McLoughlin and Guppy; p. 14; figure 9 (lower part).

Holotype

WAM P.88.15 (Figures 5E,F); Broome Sandstone (Neocomian-Barremian); Gantheaume Point, Broome, Canning Basin, Western Australia.

Etymology

Genus: after Roebuck Bay near Broome. Species: denoting frond shape.

Material

WAM P.88.15.

Distribution

Broome Sandstone (Neocomian-Barremian); Canning Basin.

Combined diagnosis for genus and species

Frond oblanceolate, margin entire, apex rounded, base acute, petiolate. Single robust vein in petiole, repeatedly dichotomous and gently divergent across lamina. Veins terminate at apex or distal part of lateral margin. Longitudinally elliptical sori inserted in depressions and arranged in 1–2 rows between each pair of veins on distal portion of frond.

Description

Single available spatulate frond 13 mm wide, 56 mm long. Frond margin entire, apex rounded, base tapering acutely to a 15 mm long petiole (Figure 5E). Single vein emerges from base, bifurcates up to five times. Veins gently diverge distally, terminating at apical margin or distal part of lateral margin; no anastomoses, no marginal vein. Sori impressions evident on distal portions of leaf (best seen on latex cast). Sori elliptical, inserted in depressions, reaching 0.5 mm wide, 2 mm long, arranged in 1–2 rows between adjacent veins (Figure 5F). Sori have granular appearance (on casts) but details of sporangia or spores unavailable.

Comments

Although only a single leaf of the type species is known, the specimen is deemed sufficiently distinctive to warrant the erection of a new genus and species. Superficially, the specimen resembles a ginkgophyte leaf in terms of its divergent dichotomous venation. However, Mesozoic ginkgophytes typically have broadly flabellate, leaves with much finer and more closely spaced venation (Sah 1952, 1953; Baksi 1968; Mehta and Sud 1953; Sah and Jain 1965; Bose 1958; Bose and Sukh Dev 1960; Anderson and Anderson 1989).

The Broome Sandstone specimen is clearly a pteridophyte owing to the presence of rows of elliptical sori between the ultimate veins. Species of the extant tropical epiphytic or lithophytic vittariacean fern genus *Antrophyum* Kaulfuss, 1824 have pendant spatulate fronds similar to *Roebuckia* but their veins are commonly reticulate with flanking dichotomous or reticulate sori (Clifford and Constantine 1980; Piggott 1988). *Roebuckia spatulata* resembles individual oblanceolate pinnules of *Adiantopteris oshimaensis* Kimura, Ohana and Aiba 1990 but is a larger leaf with more robust and less dense venation.

Incertae sedis

Genus Aculea Douglas, 1973

Type species

Aculea bifida Douglas, 1973; Lower Cretaceous; Boola Boola Forest; Victoria.

Aculea bifida Douglas, 1973 Figure 5D

cf. 1961 *Stenopteris tripinnata* (Walkom); White; p. 302; plate 4, figure 6. [1961a].

Holotype

GSV60879 (Geological Survey of Victoria), Strzelecki Group, Zone B (Neocomian); Boola Boola Forest, Gippsland, Victoria.

Material

UWA120489.

Distribution

Strzelecki Group, Zones B-C (Neocomian-Aptian), Gippsland Basin, Victoria (Douglas 1973); Broome Sandstone (Neocomian-Barremian), Canning Basin, Western Australia.

◀ Figure 5

Description

Bipinnate, probably elliptical to rhomboidshaped frond. Rachis slender (<1 mm wide) with prominent central longitudinal ridge (on impressions). Pinnae lanceolate, reaching 6 mm wide, 35 mm long, departing rachis at 20°–25°, alternate. Pinnules, needle-like or slightly flattened (Figure 5D), sub-opposite to alternate, <1 mm wide, reaching 12 mm long, with single median vein persisting to apex; base decurrent, apex pointed acute.

Comments

Although only a single sterile frond portion is available from the Broome Sandstone, it shows the deeply dissected lamina and univeined linear pinnules typical of Early Cretaceous Victorian examples of Aculea bifida (Douglas 1973; Drinnan and Chambers 1986). Dissected foliage of this type had previously been assigned to Sphenopteris or Stenopteris species (Seward 1904; Chapman 1909). White's (1961a) Stenopteris tripinnata (Walkom) from the Cronin Sandstone is comparable to A. bifida although her figured specimen appears to have more numerous pinnules arranged in a more regular bipinnate fashion. Walkom's (1919a) Stenopteris laxum (Tenison-Woods) from the Maryborough Basin may also belong to this species. The Indian Sphenopteris metzgeroides Harris of Bose and Banerji (1984) and Antarctic S. nordenskjoldii Halle, 1913 may be synonymous with A. bifida based on frond morphology but both lack fertile material comparable to the Australian species.

Genus Sphenopteris (Brongniart) Sternberg, 1825

Type species

Sphenopteris elegans (Brongniart) Sternberg, 1825; Carboniferous; Silesia.

Discussion

Numerous species have been assigned to this cosmopolitan form genus based on subtle differences in pinnule shape and venation pattern. Sphenopterid fronds may represent foliage of true ferns or seed ferns in the absence of fertile material. They are here assigned to the Pteridophyta based on the occurrence of fertile sphenopterid foliage found in coeval strata elsewhere in Australia (Drinnan and Chambers 1986).

Sphenopteris warragulensis McCoy, (in Stirling) 1892 Figure 5C

1993 Sphenopteris sp. A; McLoughlin and Guppy; figure 3.

Neotype

NMVP21341 (National Museum of Victoria), Strzelecki Group, Zone C (Barremian–Aptian); Jeetho Valley, Victoria. Designated by Douglas (1973).

Material

WAM P.89.176.

Distribution

Broome Sandstone (Neocomian-Barremian), Canning Basin.

Description

Fragmentary frond at least tripinnate, gross shape uncertain. Rachis reaching 1.5 mm broad with a prominent central longitudinal groove (on mould). First-order pinnae ovate to lanceolate bearing alternately arranged second-order pinnae proximally but giving way to ultimate pinnules distally (Figure 5C). Lanceolate second-order pinnae depart midrib at about 20°. Lanceolate ultimate pinnules arise from second-order pinnae alternately at about 20°, bases decurrent, apices pointed acute, margins entire. Venation sphenopteroid but poorly defined.

Comments

The single Broome Sandstone specimen compares favourably with Sphenopteris warragulensis McCoy, (in Stirling) 1892 from Victoria (McCoy in Stirling 1892; Douglas 1973; Drinnan and Chambers 1986) although the details of the fine serrations on pinnules are poorly defined and sori are not preserved. Medwell's (1954a) Sphenopteris hislopi Oldham and Morris probably also belongs to S. warragulensis. The narrow, elongate, acutely inserted pinnules differentiate this form from most other Sphenopteris species. Walkom's (1919a) S. flabellifolia Tenison-Woods, 1883 from the Queensland Cretaceous is closely comparable to S. warragulensis and would have nomenclatural priority if examination of the Oueensland and Victorian specimens established their conspecificity.

South American sphenopterid fronds (Herbst 1964; Baldoni 1980a; Baldoni and de Vera 1980; Petriella and Arrondo 1984) generally differ from *S. warragulensis* by their squat rhomboid or elliptical pinnules. Many Indian Jurassic-Cretaceous sphenopterid species can also be separated from *S. warragulensis* by their more compact elliptical to rhomboid pinnules (Jain 1968; Bose 1958; Bose and Sah 1968). Roy's (1968) *S. specifica* (Feistmantel) appears to have a lesser degree of frond dissection and more elliptical or oblanceolate ultimate pinnules than *S. warragulensis*.

Sphenopteris sp. A Figures 5G,H

- 1961 'Neorhachopteris minuta' White; p. 303; plate 5, figure 4. [1961a].
- cf. 1961 Ruffordia mortoni Walkom; White; p. 304; plate 5, figures 6, 7. [1961a].
- 1993 Sphenopteris sp. B; McLoughlin and Guppy; figure 8.

Material

WAM P.64.14, WAM P.89.167, WAM P.89.170, WAM P.89.173, WAM P.89.175 WAM P.89.186.

Distribution

Broome Sandstone (Neocomian-Barremian), Canning Basin.

Description

Frond elliptical, at least bipinnate, 50 mm wide, 85 mm long. Rachis stout (2 mm wide) at base, tapering distally, straight or slightly sinuous. Pinnae arranged alternately at 35°–50° to rachis, linear or arched distally, reaching 4 mm wide, 50 mm long (Figure 5H). Rachilla with prominent central longitudinal ridge (on moulds). Pinnules inserted alternately by contracted or slightly decurrent base. Pinnules rhomboid to elliptical, reaching 2 mm wide, 4 mm long; apices rounded (Figure 5G). Venation dichotomous and gently divergent from base.

Comments

This species is distinguished from *S. warragulensis* by its small elliptical to rhomboid rather than lanceolate pinnules. *Sphenopteris travisi* Stirling and *Sphenopteris* sp. of Drinnan and Chambers (1986) and *Ruffordia mortoni* Walkom, 1928 have more deeply dissected pinnules than *Sphenopteris* sp. A. The Jurassic *Coniopteris* sp. of Hill *et al.* (1966) has similar small rhomboid pinnules but *Sphenopteris* sp. A has much longer and proportionately narrower pinnae.

Herbst's (1964) Argentinian Sphenopteris sp. has more rounded pinnules than the Western Australian form but the incomplete specimens of the former inhibit close comparisons. Kasat's (1970) Cladophlebis sp. cf. C. longipennis Seward from the Indian Early Cretaceous has a very similar gross frond structure to Sphenopteris sp. A but its pinnules possess distinct midribs. Other Indian and South African Sphenopteris species figured by Jain (1968), Sukh-Dev (1972a), Bose and Sah (1968), and Anderson and Anderson (1985) differ from the Western Australian specimen by their undulate, toothed, or deeply dissected pinnules.

Incertae sedis

Genus Thinnfeldia Ettingshausen, 1852

Type species

Thinnfeldia rhomboidalis Ettingshausen, 1852; Early Jurassic; Steierdorf, Germany.

Thinnfeldia cf. talbragarensis Walkom, 1921b Figures 6A,B

- 1944 *Thinnfeldia talbragarensis* Walkom; Walkom; p. 203; plate II, figure 8.
- 1993 Thinnfeldia sp.; McLoughlin and Guppy; figure 10.

Material

UWA16690, UWA10472C.

Distribution

Leederville Formation and Bullsbrook Formation (Neocomian-Barremian), Perth Basin.

Description

Frond at least bipinnate, >90 mm long, 60 mm wide, elliptical. Rachis robust (<3 mm wide), longitudinally striate. Pinnae opposite, ovate to elliptical, L:W ratio 2:1 to 4:1, arising from rachis at 60°–80°. Pinnae range from undulate-margined to deeply dissected into 4–7 pinnules (Figure 6A). Pinnule arrangement catadromous. Pinnules elliptical, wide-obovate, or rhomboid, reaching 5 mm wide, 8 mm long; subopposite to alternate; apex rounded; base decurrent; venation odontopteroid (Figure 6B).

Comments

Walkom (1944) assigned material from the Leederville Formation to Thinnfeldia talbragarensis, a species erected for Jurassic fronds from New South Wales, but these specimens, together with additional specimens from the Bullsbrook Formation, differ from the eastern Australian form in having ovate-elliptical rather than lanceolate pinnules. Walkom's (1944: plate II, figure 8) illustration appears to be upside-down. Thinnfeldia media Tenison-Woods, 1883 figured by Jack and Etheridge (1892) from the Burrum Coal Measures, Queensland, and the Victorian Thinnfeldia sp. cf. T. indica Feistmantel, 1876 of Drinnan and Chambers (1986) which is probably synonymous with T. maccoyi Seward, 1904 differ from the Western Australian fronds by their less-dissected lanceolate pinnules.

The Western Australian specimens bear some similarities to *Ruflorinia pilifera* Archangelsky, 1964a from the Cretaceous of Argentina, however, the former specimens lack cuticular details necessary for close comparison to the South



American species. *Thinnfeldia indica* of Zeba-Bano et al. (1979) has proportionately more elongate and less dissected leaves than *T*. sp. cf. *T. talbragarensis*. However, Jain's (1968) ?*Dicroidium* specimen from the Early Cretaceous of eastern India has very similar pinnule shapes and venation to the Western Australian fronds and may be conspecific.

Incertae sedis

Order Pentoxylales

Family Pentoxylaceae

Genus Taeniopteris Brongniart 1832

Type species

Taeniopteris vittata Brongniart, 1832; Jurassic; Whitby, England.

Taeniopteris daintreei McCoy, 1874 Figures 6C,F,G; 7A

- 1944 Taeniopteris spatulata McClelland; Walkom; p. 203; plate II, figure 9.
- 1961 *Taeniopteris* cf. *T. elongata* Walkom; White; p. 303; plate figures 1B, 2B. [1961a].
- 1993 Taeniopteris daintreei; McLoughlin and Guppy; figure 14; figure 18.

Lectotype

NMVP12270 (National Museum of Victoria); Strzelecki Group, Zone C (Valanginian–Albian); Cape Paterson, Victoria. Selected by Drinnan and Chambers (1985).

Material

WAM P.64.12, WAM P.64.15, WAM P.74.26, WAM P.74.27, WAM P.74.28, WAM P.74.29, WAM P.74.32, WAM P.74.33, WAM P.74.34, WAM P.88.8. UWA16685, UWA16682, UWA16683, UWA10374A,B,E, UWA10375, UWA10376, UWA-10461A,B,C, UWA10463, UWA10464B,F,G,J,K, UWA10466A, UWA10470C,D, UWA10472B, UWA10474A, UWA10477A,C.

Distribution

Widespread; probably upper Lower Jurassic to Lower Cretaceous of Australasia. Western Australia: Broome Sandstone, Canning Basin; Cronin Sandstone, Officer Basin; Bullsbrook and Leederville Formations, Perth Basin.

Description

Leaves simple, up to 2 cm wide and 8.3 cm long, lorate, linear, or spatulate. Margin entire or gently undulate, apex rounded obtuse, base tapering acute, petiolate. Midrib longitudinally striate, robust (up to 2 mm wide), gently tapering distally, persistent. Secondary veins closely spaced, depart midrib at >60°, bifurcate once or twice then pass straight to margin at 75°–90°. Lamina rarely shows undulate folds. Attached fertile organs and cuticle unavailable.

Comments

Drinnan and Chambers (1985) provided a detailed account of this Early Cretaceous species based on material from Victoria. They suggested a relationship between T. daintreei leaves and both the pollenate fructification Sahnia laxiphora Drinnan and Chambers, 1985 and the ovulate pentoxylalean fructification Carnoconites cranwellii Harris, 1962, based on their co-occurrence in the Koonwarra fossil bed of the Gippsland Basin and similar cofossilized forms in New Zealand, New South Wales and India (Blashke and Grant-Mackie 1976; White 1981; Visshnu-Mittre 1953; Rao 1981). Drinnan and Chambers (1985) provisionally excluded White's (1981) New South Wales Jurassic Taeniopteris spatulata McClelland, 1850 from T. daintreei due to the discrepancy in the ages of the Victorian and New South Wales specimens. Differences in the preservation of associated fruiting bodies also inhibited close comparison. However, Drinnan and Chambers (1985) noted that previous distinctions between Victorian Cretaceous T. daintreei and Indian Jurassic-Cretaceous T. spatulata cuticle morphologies are probably less significant than initially suggested (Rao 1943; Douglas 1969; Visshnu-Mittre 1957). The Western Australian specimens are morphologically indistinguishable from Victorian T. daintreei leaves.

Taeniopteris daintreei-like leaves are common components of several other Middle Jurassic to Early Cretaceous floras within Australia and New Zealand (Dun 1898; Walkom 1919b, 1944; Glaessner and Rao 1955; White 1961a, b; Gould 1980; Blaschke and Grant-Mackie 1976). Several authors (e.g., Chapman 1909; Glaessner and Rao 1955, Douglas 1969; Baldoni and de Vera 1980; Drinnan and Chambers 1985) have figured or described leaves which show varying degrees of lamina dissection, in some cases making them gradational with forms attributable to *Nilssonia*

Figure 6 A,B, Thinnfeldia cf. talbragarensis Walkom, 1921; (A) UWA16690, Portion of frond, Leederville Formation, x 1; (B) UWA10472C, Isolated pinna, Bullsbrook Formation; x 4; C,F,G, Portions of variably dissected Taeniopteris daintreei McCoy, 1874 leaves; (C) UWA24640B, Bullsbrook Formation, x 1.5; (F) UWA120484, Broome Sandstone, x 3; (G) WAM P.74.26a, Bullsbrook Formation, x 1.5; D,E,H,I, Ptilophyllum cutchense Morris (in Grant) emend. Bose and Kasat, 1972; (E) WAM P.88.7, Broome Sandstone, x 2; (H) WAM P.88.4, Broome Sandstone, x 0.9; (I) UWA118836, Bullsbrook Formation, x 3.

Brongniart 1825. Several specimens from the Bullsbrook Formation also display variable dissection but differ from *Nilssonia* species herein which show distinct gaps between lamina segments (pinnules).

Incertae sedis

Pinnate frond Figure 6D

Material UWA10475.

36

Distribution

Bullsbrook Formation (Neocomian–Barremian), Perth Basin, Western Australia.

Description

A single poorly preserved pinnate frond of uncertain affinities occurs in the Bullsbrook Formation assemblage. Frond 4 cm long, 2.2 cm wide, base and apex absent. Rachis broad (3 mm), longitudinally striate, gently tapering distally; pinnules linear with full basal attachment, margins entire or gently undulate, venation indistinct (Figure 6D).

Remarks

This specimen may represent a fern, seed-fern, or cycadophyte frond. The apparently undulate margins on some pinnules invite comparison to Douglas's (1969) *Pachypteris austropapillosa* recorded from coeval "Zone B" floras of the Victorian Early Cretaceous but the specimen is too poorly preserved for identification.

Division Cycadophyta

Order Bennettitales

Genus Nilssonia Brongniart, 1825

Type species

Nilssonia brevis Brongniart, 1825; Rhaetian; Hoer, Sweden.

Nilssonia sp. A Figure 7F

1993 Nilssonia sp. A; McLoughlin and Guppy; p. 14; figure 15.

Material

WAM P.96.3.

Distribution

Nanutarra Formation (Neocomian-?Aptian), Carnarvon Basin.

Description

Fragmentary pinnate fronds with broad striate rachis (<5 mm wide). Pinnules subopposite, truncate elliptical, semicircular, oblong, or slightly falcate, up to 15 mm wide and 25 mm long; apex rounded, asymmetrical; full basal attachment; inserted laterally? or adaxially? on rachis (Figure 7F). Pinnule bases expanded slightly, basiscopic margin rounded convex, acroscopic margin straight or slightly concave. Generally >10 veins arising from pinnule base, each bifurcates no more than twice (rarely more than once), passing subparallel to apical and lateral margins without anastomoses.

Comments

The full basal insertion of pinnules on the rachis distinguishes this leaf-form from *Otozamites* species which have pinnules with contracted bases (Taylor and Taylor 1993). White's (1961b) *Pterophyllum fissum* Feistmantel leaves are pinnatifid in contrast to the pinnate *Nilssonia* sp. A. Several *Nilssonia* and *Ctenozamites* species from the Yorkshire Jurassic (Harris 1964) have similar sized fronds to the Western Australian examples but differ in the details of their pinnule shapes and venation.

Nilssonia sp. B Figure 7B

1993 Nilssonia sp. B; McLoughlin and Guppy; p. 14; figure 17.

Material

WAM P.88.5, WAM P.88.6.

Distribution

Broome Sandstone (Neocomian-Barremian), Canning Basin.

Description

Fragmentary elliptical to oblanceolate pinnate fronds, petiolate; rachis up to 2 mm wide. Pinnules with full basal attachment, semicircular to oblong, apex rounded. Basiscopic margin of pinnules gently convex, acroscopic margin straight or slightly concave (Figure 7B). Pinnules alternate, up to 12 mm wide, 22 mm long. Numerous closely spaced, fine, indistinct, veins emerge from rachis, diverge gently towards apex and lateral margins; bifurcations rare, anastomoses absent.

Comments

This leaf form differs from *Nilssonia* sp. A by its more divergent and closely spaced venation. White's (1961a) and Walkom's (1919a) *Nilssonia schaumbergensis* Dunker from the Broome Sandstone and Burrum Coal Measures respectively

both have broader and shorter lamina segments than either of the Western Australian Nilssonia species described here. White's (1981) Nilssonia compta (Phillips) Brongniart also has substantially shorter wedge-shaped pinnules. By contrast, Nilssonia plutovillensis Walkom, 1928 has narrower pinnules with more acute apices.

Genus *Ptilophyllum* Morris emend. Bose and Kasat, 1972

Type species

Ptilophyllum acutifolium Morris, (in Grant) 1840; Early Cretaceous; south of Charivar Range, India.

Discussion

Otozamites Braun, in Münster 1843 is traditionally distinguished from *Ptilophyllum* by the asymmetrical, expanded (auriculate) bases of its pinnules (Seward 1917). However, the genera may be synonymous as several *Ptilophyllum* species also possess asymmetrical auriculate pinnules (Bose and Kasat 1972). In the absence of cuticular data, Western Australian bennettitalean fronds with narrow pinnules can be compared with a wide range of Otozamites and *Ptilophyllum* species (Bose and Kasat 1972; Bose 1974).

Ptilophyllum acutifolium Morris, (in Grant) 1840 Figures 7I,J

- 1961 Zamites sp.; White; p. 305; plate 8, figure 3. [1961a].
- 1993 Ptilophyllum acutifolium; McLoughlin and Guppy; p. 14; figure 16.

Lectotype

V21330, British Museum (Natural History); Jabalpur Series equivalents (Lower Cretaceous); Kutch, India. Selected by Bose and Kasat (1972).

Material

WAM P.64.16, WAM P.89.162 WAM P.96.2, WAM P.96.4.

Distribution

Lower Cretaceous of India; possibly Jurassic and Lower Cretaceous of South America; Nanutarra Formation, Carnarvon Basin; Broome Sandstone, Canning Basin (both Lower Cretaceous), Western Australia.

Description

Fragmentary, broadly elliptical pinnate fronds. Rachis stout (1–2.5 mm wide). Pinnules subopposite to alternate, linear, straight or arched distally, inserted on adaxial surface of rachis at 30°-65°, up to 3 mm wide, 40 mm long (Figures 7I,J). Pinnule bases rounded, apices pointed acute or truncate. Pinnules aligned in a common plane or slightly imbricate. Several veins enter base of pinnules, diverge slightly, pass straight to apical margin, no anastomoses.

Comments

Ptilophyllum acutifolium is distinguished from other bennettitalean fronds in the collection by its very narrow and elongate pinnules which may be straight or gently falcate. This species is common within the Broome Sandstone and Nanutarra Formation and was identified by White (1961a) as Zamites sp. Ptilophyllum acutifolium is widely recorded from the Indian Early Cretaceous (Morris in Grant 1840; Feistmantel 1877a, b, c, 1879; Sahni and Rao 1933; Bose and Kasat 1972; Sukh-Dev and Zeba-Bano 1980; Baksi and Naskar 1981; Bose and Banerji 1984). South American Jurassic and Early Cretaceous fronds have also been assigned to this species (Arrondo and Petriella 1980; Longobucco et al. 1985) although both the Australian and South American forms tend to have longer pinnules than the Indian examples.

Ptilophyllum cutchense Morris, (in Grant) emend. Bose and Kasat 1972 Figures 6E,H,I; 7C,D

- 1944 Ptilophyllum pecten (Phillips); Walkom; p. 204; plate II, figure 6.
- 1961 Ptilophyllum pecten (Phillips); White; p. 302– 305; plate 6, figure 3D; plate 8, figure 1. [1961a].
- 1961 Otozamites bengalensis Oldham and Morris; White; p. 305; plate 7, figure 5. [1961a].
- 1993 Otozamites bengalensis; McLoughlin and Guppy; p. 14; figures 13, 14.

Lectotype

V20191 (9943), British Museum (Natural History); Rajmahal Series equivalents (?Lower Cretaceous); Kutch, India. Selected by Bose and Kasat (1972).

Material

WAM P.64.6, WAM P.64.7, WAM P.64.8, WAM P.64.13, WAM P.70.46, WAM P.86.57, WAM P.86.172, WAM P.88.4, WAM P.88.7, WAM P.88.11, WAM P.89.169, UWA16684, UWA118836.

Distribution

Broome Sandstone, Canning Basin; Leederville and Bullsbrook Formations, Perth Basin (all Neocomian-Barremian).



Description

Fronds linear, pinnate, petiolate, up to 16 mm wide, 155 mm long. Rachis stout, up to 1 mm thick. pinnules inserted adaxially on rachis. Pinnule base slightly auriculate or contracted (Figure 7C). Adjacent pinnules slightly imbricate. Pinnule bases abutting alternately on adaxial surface of rachis forming a zig-zag pattern on impressions (Figures 6E, 7D). Pinnules oblong or falcate, apices pointed acute, slightly inclined distally (Figures 6H,1). pinnules arise at 50°–70° from rachis, reaching 8 x 2 mm. Veins emerge from centre of pinnule base, dichotomize, slightly diverge, intersect apical and lateral margins without anastomoses.

Comments

In gross morphology these fronds are similar to a number of bennettitalean foliage species including ptilophyllum pecten (Phillips) Harris, 1969, P. horridum Roy, 1963, P. cauthifera Douglas, 1969, and Otozamites exhistopi Bose, 1974. However, the contracted pinnule bases, slightly expanded basiscopic pinnule lamina, pinnule imbrication, and relatively short, slightly falcate pinnules with obtuse apices suggests that the Western Australian specimens are better assigned to P. cutchense Bose and Kasat, 1972, a common Jurassic? to Early Cretaceous species of India and Australia (Walkom 1944; Glaessner and Rao 1955; White 1961a,b; Bose and Kasat 1972). Most previous Australian studies have assigned such remains to Otozamites bengalensis (Oldham and Morris) Schimper, 1870 but Bose and Kasat (1972) transfered the type specimens of that species to P. cutchense. Walkom's (1917a, 1919a) Ptilophyllum pecten specimens from the Lower Cretaceous Stanwell and Burrum Coal Measures may also belong to P. cutchense based on pinnule morphology.

Several Otozamites species identified by Walkom (1921b) from the Yarragadee Formation, northern Perth Basin, have much broader and either substantially longer or shorter pinnules than *P. cutchense* and are probably of Middle to Late Jurassic age based on palynological studies of that unit (Backhouse 1988).

Ptilophyllum boolensis (Douglas) Douglas, 1969 Figure 7G

1993 Ptilophyllum boolensis; McLoughlin and Guppy; p. 14; figure 21.

Holotype

GSV58781 (Geological Survey of Victoria); Strzelecki Group, Zone B (Neocomian); Boola Boola Forest, Gippsland, Victoria (Douglas 1969).

Material

WAM P.96.13.

Distribution

Broome Sandstone (Neocomian-Barremian), Canning Basin; Strzelecki Group, Zone B (Neocomian), Victoria.

Description

Single diminutive lanceolate pinnate frond fragment preserved as an impression in siliceous siltstone. Rachis slender (<1 mm wide). Pinnules attached to upper surface of rachis. Pinnules very small (<3 mm wide, <5 mm long), circular to elliptical, bases truncate to auriculate, apices broadly rounded (Figure 7G). Pinnules inserted alternately at about 50° to rachis; adjacent pinnules slightly overlap producing a zig-zag pattern along rachis. Single vein enters centre of pinnule base and dichotomizes two or three times, ultimate veins diverging straight to lateral and apical margins.

Comments

Although Douglas' (1969) *Ptilophyllum boolensis* specimens were defined partly on cuticular features not available for the Western Australian specimens, the Broome Sandstone frond (Figure 7G) appears to be attributable to this species based on its size and circular to elliptical pinnules. *Otozanuites pecten* Sitholey, 1984 from the ?Jurassic of India is a similar diminutive frond with rounded, partly overlapping, pinnules. Furthermore, its squat, sinuous-walled, papillate

◀ Figure 7

A, Tacuiopteris daintreei McCoy, 1874; WAM P.64.15; Broome Sandstone; x 2; B, Nilssonia sp. B; Base of frond; WAM P.88.5; Broome Sandstone; x 2; C,D, Ptilophyllum cutchense Morris (in Grant) emend. Bose and Kasat, 1972; (C) UWA16684, Leederville Formation, x 1.5.; (D) WAM P.88.172; Broome Sandstone; x 1; E, Zaniles sp.; isolated pinnule; UWA118826; Bullsbrook Formation; x 2; F, Nilssonia sp. A; fragmentary pinnules; WAM P.96.3; Nanutarra Formation; x 1.5; G, Ptilophyllum boolensis (Douglas) Douglas, 1969; WAM P.96.13; Broome Sandstone; x 6; H, Araucaria sp. B; WAM P.90.1; latex cast of axis with imbricate leaves; Broome Sandstone; x 5; I,J, Ptilophyllum acutifolium Morris (in Grant), 1840; (I) WAM P.96.2, apical portion of frond, Nanutarra Formation, x 2; (J) WAM P.89.162, Broome Sandstone, x 1; K, silicon cast of Araucaria sp. A; slender branches with elongate rhomboid leaves; WAM P.96.7; Broome Sandstone; x 3.

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epidermal cells are closely comparable to the epidermal/cuticular morphology of *P. boolensis* suggesting a close relationship. *Ptilophyllum boolensis* is restricted to Douglas' (1969) "Zone B" flora in Victoria and its occurrence within the Broome Sandstone suggests that this unit is, at least partly, also of Neocomian age.

Genus Zamites Brongniart, 1828

Type species

Zamites gigas (Lindley and Hutton) Morris, 1843; Jurassic, Scarborough, England. Selected by Andrews (1970).

> Zamites sp. Figure 7E

Material

UWA118826.

Distribution

Bullsbrook Formation, Perth Basin (Neocomian-Barremian).

Description

Linear pinnule 46 mm long, 5 mm wide, base contracted, apex rounded obtuse, margin entire (Figure 7E). Several veins emerge from base, rarely dichotomize immediately above base producing 10 ultimate veins which pass parallel along the lamina and slightly converge near apex. Complete frond and cuticular data not available.

Comments

The single available pinnule is similar to the linear parallel-veined leaflets of Zamites or Pseudoctenis fronds from the Early Cretaceous of South Africa (Anderson and Anderson 1985) and India (Sahni and Rao 1933) but specific identification is not possible without complete fronds or cuticular data.

Division Pinophyta

Class Pinopsida

Order Pinales

Family Araucariaceae

Genus Araucaria Jussieu 1789

Type species

Araucaria araucana (Molina) K. Koch, 1873; extant; Chile.

Discussion

Three species of Araucaria are recognized from

the Western Australian Cretaceous on the basis of leaf size and shape and axis thickness. These species may represent different portions or stages of maturity of the same plant. Until intermediate or more complete remains are found the foliage types are described separately.

Araucaria sp. A Figure 7K

1993 Araucaria sp. A; McLoughlin and Guppy; figure 22.

Material

WAM P.63.31, WAM P.96.7.

Distribution

Broome Sandstone (Neocomian-Barremian), Canning Basin.

Description

Slender terminal axes <4 mm wide, reaching 36 mm long, bearing spirally inserted simple scalelike leaves closely adpressed to axis (Figure 7K). Branches rare, irregular. Leaves small (1 mm wide, 2 mm long), elliptical, ovate, or rhomboid, with prominent ridge along midline of abaxial surface (on casts). Leaves tightly imbricate; overlapping by about one-third those in distally adjacent spiral. Leaf apices acutely pointed, commonly flexed adaxially.

Comments

Araucaria sp. A differs from other Western Australian araucarians by its very small, longitudinally elongate, rhomboid leaves that typically show a ridge along the centre of the abaxial leaf surface casts. In this respect the leaves are very similar to *Brachyphyllum* sp. of Banerji and Pal (1986) from the Upper Jurassic Sarnu Hill Formation, India. Araucarioid axes from the Yaragadee Formation (Middle to Late Jurassic), Perth Basin, described as *Pagiophyllum* or *Brachyphyllum* species or coniferous fragments by Arber (1910), Walkom (1921b), and White (1986) have narrower leaves that are not adpressed to the axis and belong to a separate araucarian species.

A number of other Australian and South American forms, including *Brachyphyllum* gippslandicum McCoy (in Stirling), 1892, Araucaria sp. of Drinnan and Chambers (1986), Brachyphyllum sp. of Baldoni (1980a), and Nothopehuen brevis Del Fueyo, 1991, are morphologically similar to Araucaria sp. A but their precise relationships will only be resolved when cuticular data and fructifications become available. Araucaria sp. B Figures 7H; 8A–C,F

1993 Araucaria sp. B; McLoughlin and Guppy; figure 26.

Material

WAM P.89.188, WAM P.89.189, WAM P.89.190, WAM P.90.1, WAM P.90.3, WAM P.96.14.

Distribution

Broome Sandstone (Neocomian-Barremian), Canning Basin.

Description

Axes slender to robust (2-9 mm wide, reaching at least 70 mm long) bearing spirally arranged, broadly rhomboid, scale-like leaves (Figures 7H, 8F). Axes linear or variably curved, giving off lateral branches at irregular intervals (Figures 8B,C). Leaves squat, remaining attached and adnate to axis, basally contiguous forming a rhomboid, pentagonal or hexagonal pattern on axis impressions (Figures 8A,C). Leaves attached to axis by broad base, apex contracted to a short (<0.5 mm) spine. Variations in the average basal width of leaves occurs along some axes reflecting seasonal growth. Leaves most often apically compressed, apparently fleshy or leathery in original state, venation indistinct. When laterally compressed, leaves slightly overlap bases of those in succeeding spiral.

Comments

Numerous Australian Mesozoic axes bearing rhomboid leaves, and often assigned to *Brachyphyllum* or *Allocladus* species (e.g., Seward 1904; Chapman 1904; Walkom 1917b, 1919a, 1921a, 1928; Medwell 1954a; Hill *et al.* 1966; Townrow 1967; White 1961a, 1981), may belong to the Araucariaceae, Podocarpaceae, Taxodiaceae, Cupressaceae, or Cheirolepidaceae. In this instance, association with araucarian cone scales favours an araucarian affinity, however, further morphological details and attached fertile material will be needed to clearly establish the affinities of *Araucaria* sp. B.

Brachyphyllum rhombicum Feistmantel of Sahni (1928) is closely comparable to Araucaria sp. B whereas his B. mamillare Brongniart has more elongate rhomboid leaves. The Early Cretaceous Indian Brachyphyllum bausaensis and B. eikaiostomum of Sukh-Dev and Bose (1974) are differentiated on epidermal/cuticular details but are otherwise difficult to distinguish from Araucaria sp. B. Baksi's (1968) Brachyphyllum rhombicum (Lindley and Hutton) Sahni is also very similar but its leaves are more axially elongate. The South African Araucaria rogersii (Seward) Anderson and Anderson, 1985 has spirally arranged rhomboid leaves similar to those of *Araucaria* sp. B. However, closer comparison is not possible owing to the lack of cuticular details or pollenate cones associated with the Western Australian material.

> Araucaria sp. C Figure 8E

Material WAM P.88.16.

Distribution

Broome Sandstone (Neocomian-Barremian), Canning Basin.

Description

Robust bifurcate axis clothed in spirally arranged?, flattened, lanceolate or linear leaves (Figure 8E). Length from base to bifurcation 14 cm, terminal branches both 8 cm long. Maximum width of axis 20 mm. Leaves reaching 4 mm wide, 30 mm long, smooth or with indistinct longitudinal striae, possibly contracted slightly at base, apices pointed acute. Detached leaf imprints on same slab reach 5 mm wide, 60 mm long.

Comments

The available specimen is too poorly preserved for close comparison to other illustrated material. It probably represents an araucarian conifer branch bearing dense, flattened, spirally arranged, lanceolate to linear leaves similar to the modern Australian Bunya Pine (*Araucaria bidwilli* Hooker, 1843). The leaves and branched axis of *Araucaria* sp. C are much more robust than the other species of *Araucaria* described from the Broome Sandstone.

Araucarian cones Figure 8D

Material

WAM P.89.185, WAM P.89.187.

Distribution

Broome Sandstone (Neocomian-Barremian), Canning Basin.

Description

Two cone impressions available, both c. 5×4 cm, longitudinally elliptical in outline (Figure 8D). Cones feature >15 transverse ridges (on casts) marking positions of closely spaced cone scale spirals (ridges 1.5 mm apart). Individual cone scales poorly differentiated, apices extended as 6 mm long flanges or spines that arch distally at



periphery of cone. Cone attachment point not evident. Seeds and foliage not available.

Comments

Both of the Broome Sandstone cones are isolated and can not be linked to any of the araucarian foliage species described above. Latex casts failed to reveal significant morphological details of cone scale shapes although their large size suggests that the cones are ovulate rather than pollenate. Anatomical details are not preserved in the Western Australian specimens preventing comparison to permineralized araucarian cones from the Jurassic? of India (Bohra and Sharma 1980). An araucarian cone from the Kennedy Ranges (Merlinleigh Sandstone: Eocene), Western Australia, figured by McLoughlin and Hill (in press) is of similar dimensions but has more distinctive cone scale impressions which in some cases have left prominent spirally arranged rhomboid scars on the cone axis.

Araucarian cone scales Figures 9A,B

1993 Araucarian cone scale; McLoughlin and Guppy; figure 20.

Material

WAM P.96.5, WAM P.96.6.

Distribution

Broome Sandstone (Neocomian-Barremian), Canning Basin.

Description

Detached cone scale complex (fused ovuliferous scale, seed, and bract). Scale cuneate, base pointed acute to truncate, apex truncate, no terminal spine evident (though possibly removed); width 13 mm, length 12–14 mm. Scales with elliptical to oblong indentation or cast (2.5 mm wide, 8 mm long) near base marking position of seed (Figures 9A,B). Cone scale narrowly winged.

Comments

Two cone scales are preserved in the Broome Sandstone assemblages. Similar isolated cone scales are found throughout Gondwanan Jurassic and Cretaceous strata but their affinities with foliagebased species are generally indeterminate. The Broome specimens lack apical spines in contrast to most South American and eastern Australian cone scales (Walkom 1919a; Baldoni 1981; Drinnan and Chambers 1986). They also appear to have poorly developed lateral membraneous wings although this may be a preservational flaw. The Broome cone scales are most similar to *Araucarites* sp. B of Seward (1904) and the "winged seed type 1" of Drinnan and Chambers (1986). Indian Mesozoic cone scales assigned to *Araucarites parsorensis* Lele, 1955 and Baksi's (1968) *A. cutchensis* Feistmantel are not as apically expanded as the Western Australian specimens. *Araucarites janaianus* Bose and Banerji, 1984 is similar in size and ovule position to the Western Australian scales but it possesses distinct apical spines.

Family Podocarpaceae

Genus Elatocladus Halle emend Harris, 1979

Type species

Elatocladus heterophylla Halle 1913; ?Lower Jurassic or ?Lower Cretaceous; Hope Bay, Antarctic Peninsula.

Elatocladus ginginensis sp. nov. Figures 9C–E,G

- 1961 *Elatocladus plana* (Feistmantel); White; p. 302–303; plate 6, figures 1A, 2A. [1961a].
- 1993 *Rissikia* sp.; McLoughlin and Guppy; p. 14; figure 24.

Holotype

UWA16703; Leederville Formation (Neocomian-Barremian); Cheriton Creek, Gingin, Western Australia.

Material

WAM P.88.14, WAM P.89.174, WAM P.89.192, WAM P.96.10, UWA10464C-E, UWA10466B-E, UWA10467A,B, UWA10468A, UWA10474B, UWA10475, UWA10477B, UWA16703.

Distribution

Broome Sandstone, Canning Basin; Leederville and Bullsbrook Formations, Perth Basin (all Neocomian–Barremian).

Diagnosis

Slender distal shoots bearing universed, spirally inserted, basally twisted, linear leaves in distichous

Figure 8 A-C, F, Araucaria sp. B; latex casts of branches bearing spirally arranged rhomboid leaves; (A) WAM P.89.188, x 4; (B) WAM P.89.189, x 3; (C) WAM P.89.189, x 2; (F) WAM P.89.188, x 6; all from Broome Sandstone; D, Araucarian cone impression; distal end at top of figure; WAM P.89.187; Broome Sandstone; x 1.5; E, Araucaria sp. C; large branched axis impression with overlapping scale-like leaves; WAM P.88.16; Broome Sandstone; x 0.8.



arrangement. Leaves flattened; apices bluntly rounded; bases slightly contracted to slightly decurrent.

Description

Slender terminal axes (reaching 3 mm wide and 51 mm long) bearing numerous univeined linear leaves (Figures 9C,E,G). Leaves spirally inserted although basally twisted to lie in a common plane. Leaves inserted on branches at 40° – 90° . Leaves up to 1 mm wide, 20 mm long, flattened, straight or slightly flexed distally, apices rounded. Leaf bases slightly contracted but not significantly petiolate, slightly decurrent (Figure 9D).

Comments

Harris 1979 emended Elatocladus Halle, 1913 to exclude the morphology of the leaf bases as a diagnostic character thus incorporating specimens previously assigned to both Elatocladus and Rissikia Townrow, 1967. It should be noted, however, that some workers (e.g., Anderson and Anderson, 1989) have maintained a distinction between these genera based on the presence of contracted leaf bases in Elatocladus and decurrent leaf bases in Rissikia. In the absence of attached reproductive organs the Western Australian material is insufficiently abundant or well preserved to resolve this taxonomic issue and the specimens are assigned to a new species within Harris' (1979) broader definition of Elatocladus. Numerous species from the Gondwanan Mesozoic attributed to Elatocladus, Rissikia, or other podocarpacean genera have often been distinguished by slight differences in leaflet size, shape, leaf arrangement, and petiole characters (Petriella and Arrondo 1984).

Elatocladus ginginensis sp. nov. lacks cuticle but is distinguished from other species by the size of its slender leaves, rounded leaf apices, and decurrent lamina bases which are not as significantly contracted as those of Elatocladus longifolium Baldoni, 1980b, E. plana (Feistmantel) Seward 1919, or Morenoa fertilis Del Fueyo, Archangelsky, and Taylor 1990. White's (1961a) Elatocladus plana specimens from the Cronin Sandstone have identical leaflet characters and are reassigned to E. ginginensis. The E. plana specimens of Glaessner and Rao (1955) from the Early Cretaceous of South Australia are described as having leaves with full basal attachment, a feature not consistent with Elatocladus. Their specimens may be synonymous with E. ginginensis although their illustrations do

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not allow close comparison. Other Australian specimens assigned to *E. plana* (Hill *et al.* 1966; Walkom 1919a); and *Rissikia talbragarensis* White, 1981 have either substantially longer or broader leaves which show a dense but regular spacing not evident in *E. ginginensis*.

Elatocladus conferta (Oldham and Morris) Sahni, E. kingianus Bose, Kutty, and 1928 and Maheshwari, 1982 specimens of Halle (1913), Sah (1965), Maheshwari and Singh (1976), Bose and Banerji (1984), and Walkom (1928) have substantially smaller leaves than E. ginginensis. Permineralized remains assigned to E. sahnii Vishnu-Mittre, 1957 from the Indian Jurassic have similar decurrent bases but the absence of anatomical details in the Western Australian specimens prevents closer comparison. Extra-Gondwanan Elatocladus species are more readily distinguishable on gross leaf morphology or cuticular details (e.g., Miller and Lapaska 1985; Kimura and Ohana 1988, 1989; Kimura et al. 1991).

Incertae sedis

Genus Carpolithes Brongniart 1822

Type species

Carpolithes thalictroides Brongniart, 1822; Tertiary; France and England.

Carpolithes bullsbrookensis sp. nov. Figures 9F,H–K

1993 *Carpolithes* sp. McLoughlin and Guppy; figure 19.

Holotype

UWA10469A; Bullsbrook Formation (Neocomian–Barremian); 2.5 km northeast of Bullsbrook Hotel, Perth Basin.

Material

UWA10374C,D, UWA10462B, UWA10464H,I, UWA10468B, UWA10469A,B–F, UWA10473A.

Distribution

Bullsbrook Formation (Neocomian-Barremian); Perth Basin.

Diagnosis

Ovate to elliptical wingless seeds, reaching 5 x 7

Figure 9 A,B, Araucarian cone scales; (A) WAM P.96.5; (B) WAM P.96.6; Broome Sandstone; both x 4; C-E, G, Elatocladus ginginensis sp. nov.; detached planated foliage-bearing twigs; (C) UWA16703, x 1.5; (D) UWA118835, x 5; (E) UWA10466C, x 2; (G) UWA10464E, x 2; all from Bullsbrook Formation; F, H-K, Carpolithes bullsbrookensis sp. nov.; seed impressions and internal casts; (F) UWA10469F; (H) UWA104688; (I) UWA10462B; (J) UWA10469C; (K) UWA10469A; all from Bullsbrook Formation; all x 8. mm, with a rounded or obtusely pointed apex and smooth surface apart from a prominent vertical ridge (on internal casts).

Description

Isolated seeds of indeterminate affinity. Seeds ovate to elliptical, reaching 5 mm wide, 7 mm long, wings absent; internal casts ovoid (Figures 9H–K). Prominent vertical ridge commonly evident on internal casts but surface otherwise lacks ornamentation (Figures 9F,J,K). Base truncate or rounded, apex rounded or closing to an obtuse point.

Comments

Seeds of this type are common in the Bullsbrook Formation and are frequently preserved in association with Taeniopteris daintreei leaves although no physical connection is evident. White (1981, 1986) figured similar though smaller seeds with a longitudinal ridge preserved in pentoxylalean (Carnoconites) cones from the Jurassic Talbragar fish beds in New South Wales. Seeds belonging to Carnoconites cranwellii Harris, 1962 fruits from the Victorian Early Cretaceous (Drinnan and Chambers 1985) are also substantially smaller (1 mm diameter) than the Western Australian seeds and differ by their polygonal outline. This may simply be due to crowding of seeds in the Victorian cones. Larger, more loosely packed Carnoconites cones may have borne more rounded seeds like White's (1981) examples from Talbragar. Seeds of Carnoconites compactum Srivastava, 1946 are similar in size although the species was defined upon permineralized material which does not clearly show the seed shape in lateral view (Sahni 1948; Vishnu-Mittre 1953). Compressed Carnoconites laxum Harris, 1962 fruits from New Zealand show only indistinct seeds not favourable for comparison to Carpolithes bullsbrookensis. Carpolithes sp. B of Bose and Banerji (1984) has a longitudinal ridge like C. bullsbrookensis but is much larger with an acute apex. Seeds belonging to Rissikia talbragarensis White, 1981 are of similar size to C. bullsbrookensis but lack a longitudinal ridge.

Winged conifer seed Figure 10A

1993 Conifer seed with wing; McLoughlin and Guppy; figure 25.

Material

WAM P.89.191.

Distribution

Broome Sandstone (Neocomian-Barremian), Canning Basin.

Description

Seed positioned basally on wing, wrinkled, ovate, c. 3.5 mm wide, 5 mm long. A flange (<1 mm wide) around lateral margins of seed expands distally to form the 8.5 x 17 mm longitudinally striate oblong wing (Figure 10A).

Comments

The single available seed impression differs from those figured by Drinnan and Chambers (1986) from the Victorian Cretaceous by its distally expanded wing. The basal part of the seed has broken away leaving only a small portion of the fertile body. The seed does not show organic connections to any other plant remains and its affinities remain uncertain.

Genus Bucklandia Presl (in Sternberg), 1825

Type species

Bucklandia anomala (Stokes and Webb) Presl (in Sternberg), 1825; Jurassic; Sussex, England.

Bucklandia sp. Figure 5E

1961 *Bucklandia* sp.; White; p. 305; plate 8, figure 2. [1961a].

1993 Bucklandia-type axis; McLoughlin and Guppy; p. 14; figure 9 (upper part).

Material

WAM P.96.8.

Distribution

Broome Sandstone (Neocomian-Barremian), Canning Basin.

Description

Axis impression bearing spirally arranged, broadly elliptical, leaf scars. Leaf scars 4 mm wide, 2 mm tall, lacking obvious vascular strands. Scars raised above surface of axis (on cast), separated by 0.5 mm grooves; arranged in 35° right-handed spirals, 50° left-handed spirals measured with respect to axial direction. Leaves and anatomical details not preserved.

Comments

The single stem fragment (upper right of Figure 5E) is similar to a number of Jurassic and Cretaceous axis casts assigned to *Bucklandia* Presl (in Sternberg), 1825. White (1961a) figured a larger axis from the same locality (Gantheaume Point, Broome) showing well developed spirally arranged elliptical leaf scars. The Western Australian examples lack the anatomical details necessary for

comparison to Indian *Bucklandia* species described by Seward (1917), Sahni (1932), Bose (1953a, b) and Sharma (1969a). Anatomically preserved *Bucklandia* axes have been associated with *Williamsonia* fructifications and *Ptilophyllum*-type foliage in India (Sahni 1932) suggesting a bennettitalean affinity. Although a *Roebuckia spatulata* frond occurs on the same slab as the *Bucklandia* specimen (Figure 5E), no connection is evident or inferred.

Ribbed axes Figure 10B

1993 Striate axis; McLoughlin and Guppy; figure 23.

Material

WAM P.63.30, WAM P.65.38, WAM P.65.43, WAM P.65.46, WAM P.65.47, WAM P.65.48, WAM P.66.3, WAM P.66.4, WAM P.66.6, WAM P.66.7, WAM P.66.8, WAM P.66.9, WAM P.66.10, WAM P.66.12.

Distribution

Broome Sandstone, Canning Basin; Bullsbrook Formation, Perth Basin (both Neocomian-Barremian).

Description

Several indeterminate longitudinally ribbed or striate axes are preserved as casts (figure 10B) and impressions. Axes reaching 4.5 cm wide, 13.5 cm long, cylindrical or flattened through compaction, commonly with external? longitudinal ribs averaging 2.5 mm apart. No axis nodes, attached leaves, fruits, or roots evident.

Comments

These axes lack diagnostic features necessary to assign them to any plant group, however, their size suggests that they may be the remains of a robust gymnosperm. The ribbed surface of some specimens invites comparison to equisetalean axes (e.g., Roy 1968; Drinnan and Chambers 1986), however, the Western Australian axes lack the transverse nodes typical of that group.

Genus Rhizomopteris Schimper, 1869

Type species

Rhizomopteris lycopodioides Schimper, 1869; Carboniferous; near Dresden, Germany.

Rhizomopteris sp. Figure 10C

Material WAM P.89.184.

Distribution

Broome Sandstone (Neocomian-Barremian), Canning Basin.

Description

Irregular ?bifurcate axis bearing circular to elliptical protuberances set in surface depressions (on mould) separated by broad ridges and folds (Figure 10C). Protuberances reaching 3 mm wide, 7 mm long, roughly arranged along axis in *en echelon* bands. Sporangia, leaves, and cuticle not evident.

Comments

A single available specimen is similar to axes figured by Seward (1904) and Chapman (1909) from the Lower Cretaceous of Victoria. Chapman (1909) inferred a relationship between his Rhizomopteris axes and Taeniopteris leaves. No such affinity can be deduced from the present material. The fossil probably represents a fern rhizome bearing circular to elliptical scars of abscissed frond rachises although no vascular traces are evident on the abscission zones. Rhizomopteris rajmahalensis Gupta, 1955 is most closely comparable to the Broome Sandstone specimen but has C-shaped rather than circular to elliptical rachis scars. Bose (1958) figured additional material comparable to Gupta's (1955) specimens and considered that the axes belonged to conifers. Coniferous axes figured by Bancroft (1913) and Sahni (1931) have transversely elongate abscission scars in contrast to the oblique or longitudinally elongate scars of Gupta's (1955), Bose's (1958), or the Broome Sandstone Rhizomopteris species.

Genus Mesembrioxylon Seward, 1919

Type species

Mesembrioxylon woburnense (Stopes) Seward, 1919; Cretaceous; Woburn, England.

Mesembrioxylon sp. Figures 10D-H

- 1993 Silicified wood with *Teredo* burrow casts; McLoughlin and Guppy; figure 1.
- 1994 Fossil wood; McLoughlin *et al.*; p. 453; figs 8a-m, 10a,b.

Material

UWA120186-UWA120237.

Distribution

The described specimens are derived from the Birdrong Sandstone (Neocomian-?Aptian), Carnarvon Basin. Other fossil woods have been reported from the Nanutarra Formation



(Neocomian-?Aptian) and Yarraloola Conglomerate (Neocomian-?Barremian) of the Carnarvon Basin, Dandaragan Sandstone (?Barremian-?Aptian) and Molecap Greensand (Cenomanian-Santonian) of the Perth Basin, and Nakina Formation (Barremian-lowermost Aptian) of the Collie Basin (Simpson 1912; Cox 1961; Playford *et al.* 1976; Hocking 1990, Buckhouse *et al.* 1995).

Description

Woods typically fragmentary, seldom exceeding 50 cm long and 15 cm diameter, randomly orientated in sediments. Woods show extensive biogenic borings (Figures 10E,H). Woods preserved by siliceous and phosphatic permineralization, strongly weathered and infiltrated by iron-oxide and clay minerals. Only secondary xylem tissues are preserved. Prominent growth banding evident (Figures 10G,H) but details of pitting arrangement on individual cell walls often poorly defined or absent (Figure 10D). Relatively sparse uniseriate xylem rays consist of 1-12 (av. 4) cells (Figure 10F). Uniseriate or rarely biseriate bordered pits are sparsely evident on radial walls of xylem tracheids. Tangential walls not pitted. Pits have oblique slitlike apertures where discernible. Growth bands variable in width (0.06-12 mm) both between and within specimens. False growth rings sporadically developed in some specimens. In most cases middle lamella (initially consisting of pectinoid compounds between the primary walls of adjacent cells) has been degraded producing a wood texture that appears to consist of detached or partially detached tracheids. Cambium, phloem, and bark tissues absent. Primary xylem and pith poorly preserved or masked by iron oxides.

Comments

The small pith content of the plants (pycnoxylic axes) suggests that the woods derive from the dominant arborescent elements of the Australian Early Cretaceous vegetation (viz., the podocarp or araucarian conifers) rather than fern, pteridosperm, or bennettitalean groups that typically contain a large proportion of pith within the stem (manoxylic axes). Permineralized wood belonging to podocarp and araucarian conifers is common in Gondwanan Cretaceous sediments (Sahni 1931; Jefferson 1983; Francis 1986; Frakes and Francis 1990; Francis and Coffin 1992) and the foliage attributable to these groups is abundant in coeval Western Australian strata. Identification of fossil conifer woods is largely based on pitting arrangements on the radial walls of longitudinal xylem tracheids and ray cells but due to poor preservation such details are not available for most Western Australian specimens. The absence of typically araucariacean closely spaced multiseriate hexagonal bordered pits on radial tracheid walls and sporadic presence of uniseriate bordered pits with oblique apertures suggests that these woods have podocarpacean affinities although cupressacean woods also have similar pitting arrangements (Greguss 1955). The prominent but variable growth banding and occasional development of false growth rings implies a distinctly seasonal climate but with considerable intra- and inter-seasonal variability McLoughlin et al. (1994).

Cox (1961) illustrated infilled molluscan borings from the Nanutarra Formation (Early Cretaceous, Carnarvon Basin) both with and without traces of associated fossil wood. The casts are probably remnants of teredinid or pholadid boring casts left behind after the degradation of coniferous driftwood. One wood specimen in the Birdrong Sandstone assemblage shows a cross-section of an unidentified bivalve preserved within an excavation chamber (Figure 10E).

Saprophytic fungi Figures 11A-l

1994 Fungi within wood; McLoughlin *et al.*; p. 455; figures 9a–l.

Material

UWA120187, UWA120217, UWA120228, UWA120229, UWA120231, UWA120232.

Distribution

Birdrong Sandstone (Neocomian-?Aptian), Carnarvon Basin.

Description

Several fossil wood specimens from the Birdrong Sandstone, Carnarvon Basin, show zones of partly degraded cells or cavities which are circular, elliptical, or irregular in transverse section and elliptical in longitudinal section. The cavities are up to 4 mm in axial length and 0.2–0.9 mm in

Figure 10 A, Winged seed with portions of base and apex removed; WAM P.89.191; Broome Sandstone; x 6; B, Cast of ribbed axis; WAM P.63.30; Broome Sandstone; x 1; C, *Rhizomopteris* sp.; WAM P.89.184; Broome Sandstone; x 2; D,F,G, *Mesembrioxylon* sp.; (D) radial section with three groups of ray cells, UWA120187, x 60; (F) tangential section showing rays generally comprising 2–4 cells, UWA120199, x 30; (G) transverse section showing transition from latewood (bottom) to earlywood (top), UWA120186, x 30; all from Birdrong Sandstone; E,H, Transverse sections of *Mesembrioxylon* wood showing variation in growth rings and intensive bivalve borings filled by calcite and/or glauconitic sand. Note preserved bivalve within bored cavity (E: arrowed); (E) UWA120220, x 2; (H) UWA120208, x 1.5; both from Birdrong Sandstone.



diameter. The degraded zones occur commonly, though not exclusively, within the latewood (Figures 11A,B,C). The cavities are either filled with secondary iron oxides or silica or occasionally contain ramifying weakly septate filaments reaching 450 μ m in length and 4–15 μ m in width (Figure 11D). The filaments branch irregularly, have an external bullate texture, and appear to contain irregularly spaced and poorly defined septa (Figures 11E–G,I). Filaments often occur in intimate contact with the degraded wood cells of the cavity margin (Figure 11F).

Comments

Such filaments and spindle-shaped wood cavities are morphologically similar to saprophytic fungal hyphae and white pocket rot cavities described from other modern and fossil woods (Blanchette 1980; Stubblefield *et al.* 1985; Stubblefield and Taylor 1986, 1988; Weaver *et al.*, in press). Jefferson (1987) figured fungal hyphae and possible spores in Early Cretaceous conifer wood from Alexander Island, Antarctica, and Halle's (1913) sketch of Mesozoic fossil wood from the Antarctic Peninsula also shows elliptical markings reminiscent of pocket rot. The Birdrong Sandstone woods incorporate the first examples of fossilized saprophytic fungi recorded from Western Australia (McLoughlin *et al.* 1994).

Other plant remains

White (1961a) figured a number of Western Australian plant macrofossils many of which have been reassigned here to different taxa on the basis of information from new material in the Western Australian Museum and University of Western Australia collections (Table 1). However, a few of her figured specimens are not matched by conspecific material in the Western Australian collections. Her Pagiophyllum peregrinum Schimper from the Callawa Formation, although similar to Araucaria sp. B, has leaves with distinctly mucronate apices. White's (1961a, plate 6, figure 4) "fine frond" is too incomplete for confident identification but it may represent the fragmentary remains of an Aculea or Sphenopteris frond or an Elatocladus terminal twig. Her Pachypteris sp., also

from the Callawa formation, is a pinna bearing oblanceolate pinnules some of which appear to have elliptical fertile bodies along their acroscopic margins. Similar fronds from the Victorian and Indian Early Cretaceous have been assigned to Onychiopsis paradoxus Bose and Sukh Dev, 1961 (Drinnan and Chambers 1986). White's (1961a) Cladophlebis albertsi (Dunker) from the Leveque Sandstone [now regarded as part of the Broome Sandstone (Yeates et al. 1984)] differs from Cladophlebis sp. cf. C. oblonga by its pointed pinnules but her specimen is too poorly preserved for close comparison to other described species. White's (1961a) Dichopteris delicatula Seward from the Broome Sandstone does not have preserved venation and may be a Sphenopteris or Cladophlebis species. Her Nilssonia schaumbergensis Dunker, also from the Broome Sandstone has pinnules of variable width. The specimen may be a Taeniopteris daintreei leaf showing irregular lamina dissection like some forms illustrated herein. White's Cycadolepis sp. from the Cronin Sandstone is too poorly preserved for definite identification. White (1961a) also mentions but does not figure several other plant taxa from the Canning and Officer Basin Lower Cretaceous including: Carpolithus circularis, Cladophlebis sp., Taeniopteris howardensis Walkom, Dictyophyllum davidi Walkom, Pterophyllum sp., Sphenopteris superba Shirley, Brachyphyllum manillare Lindley and Hutton, and Ginkgoites digitata Brongniart. These identifications (Table 1) have not been assessed in the present study.

Walkom (in McWhae *et al.* 1958) identified specimens referrable to *Nilssonia*, *Otozamites*, and *Elatocladus* from the Nanutarra Formation. The whereabouts of this material is unknown and no revision of the identifications can be attempted. However, these genera are common elements of the Early Cretaceous Broome Sandstone flora and it is likely that several species are shared between these formations. Walkom (in McWhae *et al.* 1958) also reported fossil leaves from the Yarraloola Conglomerate (Early Cretaceous, Carnarvon Basin) but provided no identifications and the location of his specimens is unknown prohibiting systematic re-evaluation.

Brunnschweiler (in Traves et al. 1956) tentatively

Figure 11 Aspects of fungal attack on, and hyphae preservation within, *Mesembrioxylon* (conifer) wood from the Birdrong Sandstone. (A) UWA120231, transverse section of wood showing fungal-degraded pockets, x 2. (B) UWA120187, transverse section of wood showing fungal-degraded pockets positioned within latewood, x 6; (C) UWA120221, transverse section of wood showing initial stages of cell breakdown and pocket formation, x 12; (D) UWA120186, details of a pocket with numerous phosphate coated fungal hyphae and a spherical body (upper left), x 60; (E) UWA120217, branched hyphae within a pocket, x 60; (F) UWA120232, details of fungal hyphae represented by a thin central filament surrounded by a bullate textured phosphate coating, x 120; (G) UWA120186, details of an expanded area near the tip of a fungal hypha, x 600; (H) UWA120132, fungal hyphae in contact with wood tracheids along the margin of a pocket, x 120; (I) UWA120232, branched fungal hyphae in pocket, x 120.

 Table 1
 Tentative revision of Lower Cretaceous plants illustrated or identified by White (1961a) from Canning and Officer Basins collections compiled during regional geological surveys of the 1950s and 1960s.

White's (1961a) identification/ illustration	Formation	Tentative revised identification
Stenopteris tripinnata Walk. (Pl. 4, fig. 6)	Cronin Sst	cf. Aculea bifida
Linguifolium denmeadi Jones and de Jersey (Pl. 5, fig. 3)	Cronin Sst	Phyllopteroides westralensis
'Neorhachopteris minuta' (Pl. 5, fig. 4)	Callawa Fm	Sphenopteris sp. A
Pagiophyllum peregrinum Sch. (Pl. 5, fig. 5)	Callawa Fm	?Araucaria sp.
Ruffordia mortoni Walk. (Pl. 5, figs 6,7)	Callawa Fm	cf. Sphenopteris sp. A
Elatocladus planus (Feist.) (Pl. 6, figs 1A, 2A)	Cronin Sst	Elatocladus ginginensis
Taeniopteris cf. elongata Walk. (Pl. 6, figs 1B, 2B)	Cronin Sst	Taeniopteris daintreei
Ptilophyllum pecten (Phillips) (Pl. 6, fig. 1D;	Cronin Sst,	Ptilophyllnm cutchense
Pl. 8, fig. 1)	Broome Sst	, ,
Cycadolepis sp. (Pl. 6, fig. 2C)	Cronin Sst	not identified
stem (Pl. 6, fig. 3)	Callawa Fm	Nathorstianella babbagensis
fine frond (Pl. 6, fig. 4)	Callawa Fm	not identified
Pachypteris sp. (Pl. 6, fig. 5)	Callawa Fm	Onychiopsis sp.
Cladophlebis australis (Morr.) (Pl. 7, figs 1,6)	Callawa Fm,	Cladophlebis cf. oblonga
	Broome Set	,
Cladophlebis albertsi (Dunk.) (Pl. 7, fig. 2)	Broome Sst	?Cladophlebis sp.
Dichopteris delicatula Sew. (Pl. 7, fig. 3)	Broome Sst	?Sphenopteris or Cladophlebis sp.
Nilssonia schaumbergensis Dunk. (Pl. 7, fig. 4)	Broome Sst	Nilssonia or Taeniopteris sp.
Otozamites bengalensis O. and M. (Pl. 7, fig. 5)	Broome Sst	Ptilophyllum cutchense
Bucklandia sp. (Pl. 8, fig. 2)	Broome Sst	Bucklandia sp.
Zamites sp. (Pl. 8, fig. 3)	Broome Sst	Ptilophyllum acutifolium
Hausmannia cf. buchii Andrae (Pl. 8, fig. 4)	Broome Sst	Hausmannia sp.
Taeniopteris sp.	Cronin Sst	not assessed
Carpolithus circularis	Cronin Sst	not assessed
Hausmannia sp.	Cronin Sst	not assessed
Cladophlebis sp.	Broome Sst	not assessed
Taeniopteris howardensis Walk.	Broome Sst	not assessed
Dictyophyllum davidi Walk.	Broome Sst	not assessed
Pterophyllum sp.	Broome Sst	not assessed
Sphenopteris superba Shirley	Broome Sst	not assessed
Brachyphyllum mamillare L. and H.	Broome Sst	not assessed
Ginkgoites digitata Brongn.	Callawa Fm	not assessed
Brachyphyllum foliage	Callawa Fm	not assessed

identified ?Johnstonia, Ginkgo, Cladophlebis, Pagiophyllum, ?Brachyphyllum, Taeniopteris, Sphenopteris, ?Samaropsis, Dictyophyllum and indeterminate wood from the Callawa Formation, Canning Basin. The presence of Johustonia (=Dicroidium) would denote a Triassic age for this unit but the identification is probably incorrect.

Brunnschweiler (1960) listed but did not describe or illustrate the following taxa from the Broome Sandstone at Gantheaume Point: Ptilophyllum pecten, Cladophlebis australis, Otozamites cf. bengalensis, Pseudocycas sp., Hausmannia sp., ?Cordaites sp., Pterophyllum sp., ?Microphyllopteris sp., Sphenopteris cf. superba Walkom, ?Dictyophyllum sp., Cladophlebis cf. albertsi, Taeniopteris cf. howardensis, and Nilssonia sp. Most of these taxa are probably attributable to species described herein. The identification of Cordaites, a Palaeozoic genus, is almost certainly incorrect. The Dictyophyllum specimens may represent fragmentary portions of Hausmannia fronds although the former is not uncommon in the Indian late Mesozoic (Bose and Jana 1979; Bose and Banerji 1984). Specimens referred to *Otozamites*, *Pterophyllum* and *Pseudocycas* may belong to one of the *Ptilophyllum* species described above.

Comparisons between the Western Australian assemblages

A significant number of plant taxa are shared between the various Western Australian Early Cretaceous formations (Table 2). Although there is evidence of intra-Australian floral provincialism in the Early Cretaceous (Dettmann *et al.* 1992), the Western Australian marginal basins all lay within latitudes of about 45°–55° during that period (Veevers *et al.* 1991) and probably experienced similar climatic conditions. Minor differences between the Western Australian assemblages are probably attributable to limited sampling, local depositional factors and environmental setting. For example, the fully fluvial Cronin Sandstone appears to contain a higher representation of gymnosperms than units deposited in deltaic or

SPECIES	LEEDERVILLE FORMATION	BULLSBROOK FORMATION	NANUT ARRA FORMATION	BIRDRONG SANDSTONE	BROOME SANDSTONE	
 Isoetites elegans	+					
Nathorstianella babbagensis					+	
Hausmannia sp.					+	
Cladophlebis cf. oblonga		+			+	
Phyllopteroides westralensis		+			+	
Microphyllopteris gleichenioides					+	
Roebuckia spatulata					+	
Aculea bifida					+	
Sphenopteris warragulensis					+	
Sphenopteris sp. A					+	
Thinnfeldia cf. talbragarensis	+	+				
Taenipteris daintreei	+	+			+	
Pinnate frond		+				
Nilssonia sp. A			+			
Nilssonia sp. B					+	
Ptilophyllum acutifolium			+		+	
Ptilophyllum cutchense	+	+			+	
Philophyllum boolensis					+	
Zamites sp.		+				
Araucaria sp. A					+	
Araucaria sp. B					+	
Araucaria sp. C					+	
Araucanan cones					+	
Flatadadua ainainanaia					+	
Campbilitas hullbrookausis	+	+			+	
Mingod conifer coods		+				
Rueklandia sp					+	
Ribbed axes					+	
Rhizowonteris sp		+			+	
Mesembriorulan sp					+	
Saprophytic fungi				+		
ouprophytic rungi				+		

Table 2 Distribution of fossil plant taxa in the studied stratigraphic units. See text for author citations.

coastal plain environments. The latter units are richer in lycophytes and pteridophytes probably owing to milder local maritime climates and wetter riparian environments, or higher water tables in lowland settings.

Relationships with other Australian floras

Other significant Australian mid- to late Mesozoic floras include the Gippsland-Otway Basin assemblages of Victoria (Douglas 1969, 1973; Drinnan and Chambers 1986), the Talbragar flora of New South Wales (Walkom 1921a; White 1981), the Eromanga, Clarence-Moreton, Laura, Styx, and Maryborough Basin floras of Queensland (Walkom 1917a,b, 1918, 1919a, 1928; Hill *et al.* 1966; Gould 1978, 1980; McLoughlin and Drinnan 1995; McLoughlin *et al.* 1995), the Bauhinia Downs flora of the Northern Territory (White 1961b), the Mt Babbage flora of South Australia (Glaessner and Rao 1955), and the Mingenew (Yarragadee Formation) flora of Western Australia (Arber 1910; Walkom 1921b). Of these, the Otway, Gippsland, and Eromanga Basin floras are the best known.

Douglas (1969, 1971) proposed four assemblage zones (Zones A-D) for Victorian Neocomian to Early Albian strata based on plant macrofossils and tied these to the independent palynostratigraphic zonation of Dettmann (1963); later refined by Dettmann and Playford (1969), Dettmann and Douglas (1976), and Helby et al. (1987). Douglas' (1969) megafloral zones are largely based on the presence or absence of key foliage species hence their recognition may be strongly influenced by local palaeoenvironmental, depositional, and seasonal factors. The collective Western Australian assemblages bear greatest similarity to Douglas' (1969) Zone B (Neocomian) flora due to the presence of the key species Taeniopteris daintreei Ptilophyllum boolensis. Phyllopteroides and westralensis is an entire-margined form similar to P.

laevis from the Victorian Zone B (and equivalent strata in Queensland). This favours an Early Cretaceous age but *P. westralensis* requires further study to determine its phylogenetic relationships with the range of eastern Australian species. Another diagnostic Victorian Zone B species, *Pachypteris austropapillosa* is absent from the Western Australian assemblages although a poorly preserved pinnate frond from the Bullsbrook Formation (Figure 6D) may be a related form.

Douglas's (1969) latest Jurassic or earliest Cretaceous Zone A floras are characterized by bennettitalean leaf forms not recognized in Western Australia. Victorian Zone B floras are also rich in bennettitaleans but only one Western Australian form (Ptilophyllum boolensis) is shared suggesting significant intra-Australian floristic provincialism. Nevertheless, the abundance of bennettitaleans in Zone B suggests better correlation with the Western Australian floras than does the succeeding Zone C where bennettitaleans are entirely absent. The Victorian Zone C (?late Neocomian to early Albian) floras also differ from the Western Australian assemblages by the presence of ginkgophytes, sphenophytes, angiosperms, and a range of distinctive pteridophyte and conifer species (Drinnan and Chambers 1986). A few species (Taeniopteris daintreei, Sphenopteris warraguleusis, and Aculea bifida) are shared between these assemblages but some of these forms may be long-ranging. Douglas' (1969) Zone D (middle-?late Albian) floras are dominated by conifer and fern species which are not represented in Western Australia. Australian Cenomanian floras mark the decline of many gymnosperm groups and diversification of the angiosperms (McLoughlin et al. 1995).

The Talbragar Fish Bed flora (Merrygoen Ironstone Member of the Purlawaugh Formation) illustrated by Walkom (1921a) and White (1981) is generally regarded as late Early Jurassic in age (Hind and Helby 1969; Gould 1975) but contains a number of superficially similar plant fossils to the Western Australian Early Cretaceous assemblages including species of Taeniopteris, Thinnfeldia, Brachyphyllum (Araucaria herein), Nilssouia, and Rissikia (= Elatocladus). However most forms can be distinguished at species level and the generic similarities may be due to palaeoecological similarities between these assemblages. The Early and Middle Jurassic floras of the Marburg Formation, Walloon Coal Measures, and equivalents in the Clarence-Moreton Basin of New South Wales and Queensland (Walkom 1915, 1917a,b, 1919b; Hill et al. 1966; Gould 1971, 1980; McLoughlin and Drinnan 1995) also share several genera with the Western Australian Cretaceous assemblages but clear species-level distinctions are apparent. Plant assemblages from the Dalrymple Sandstone, Laura Basin, initially assigned to the Cretaceous by Walkom (1928) are now regarded as Jurassic in age (Gould 1975) and only share one species (*Microphyllopteris gleichenioides*) with the Western Australian assemblages. The Middle to Late Jurassic floras of the Yarragadee Formation, Perth Basin, Western Australia (Arber 1910; Walkom 1921a; McLoughlin and Hill, in press) contain Otozamites fronds and Pagiophyllum branchlets that differ from the Early Cretaceous fossils. Several other fragmentary plant fossils have been recorded from the Yarragadee assemblages but the flora requires systematic revision.

A small plant assemblage of probable Late Jurassic age from the Hooray Sandstone in the northwestern Eromanga Basin, Northern Territory (Gould 1978), is dominated by Bennettitalean fronds (*Ptilophyllum* sp.) and conifer twigs but no species are shared with the Western Australian Cretaceous floras.

The Maryborough Formation of the Maryborough Basin, Queensland, contains a small macroflora showing some similar elements [Taeniopteris spp., Ptilopliylliim pecten (= ?Ptilophyllum cutchense)] to the Western Australian assemblages (Walkom 1918). However, the Maryborough Formation floras are more similar to the Gippsland Basin Zone C (?late Neocomian to earliest Aptian) macrofloras in terms of the conifer, ginkgophyte and equisetalean groups represented.

The Albian Burrum Coal Measure flora from the Maryborough Basin (Walkom 1919a) has a number of generic similarities to Western Australian assemblages but there are few conspecific elements. The presence of angiosperms and ginkgophytes in the Burrum flora suggests closer correlation with the Victorian Zone C–D floras. Similarly, the Styx Coal Measures of central Queensland are also characterized by the presence of angiosperms and are probably of Albian age (Walkom 1919a; Dettmann and Playford 1969; Dettmann and Douglas 1976).

The little-studied Stanwell Coal Measures west of Rockhampton, Queensland, are associated with marine strata yielding Neocomian bivalves (Skwarko 1968 and early to middle Albian palynofloras (Dettmann and Playford 1969). They also contain a macroflora consisting of Equisetites Cladophlebis sp., Phyllopteroides laevis, sp., Taeniopteris spp. (cf. Taeniopteris daintreei), Ptilophyllum pecten (cf. Ptilophyllum cutchense), Araucarites polycarpa Tenison-woods, and Elatocladus plana (cf. Elatocladus ginginensis), showing strong similarities to the Western Australian assemblages (Walkom 1915, 1917a,b; Hill et al. 1966; Cantrill and Webb 1987). Cantrill and Webb (1987) suggested a Neocomian age for the Stanwell Coal Measures owing to the occurrence of the index fossil Phyllopteroides laevis

and its distribution in Neocomian strata of the Surat and Gippsland Basins.

The floras most closely comparable to the Western Australian assemblages are those from the Algebuckina Sandstone (Eromanga Basin) at Mt Babbage, South Australia, and from the Lees Sandstone and overlying beds (Carpentaria Basin), at Bauhinia Downs, Northern Territory. The Algebuckina Sandstone incorporates Middle Jurassic to Neocomian sediments (Moore 1986; Wiltshire 1989). The macrofloras at Mt Babbage occur in the upper part of this unit and are probably of Neocomian age. Although requiring systematic revision, the Mt Babbage flora shares several taxa with the Western Australian assemblages (Glaessner and Rao 1955). Most notable are the co-occurrences of Nathorstianella babbagensis, Ptilophyllum cntchense, and Taeniopteris daintreei. (White 1961b, 1966). The Bauhinia Downs flora likewise shares several key taxa with Western Australia including Ptilophyllum cutchense, Microphyllopteris gleichenioides, Hansmannia sp., and Taeniopteris daintreei, and owing to the abundance of bennettitaleans and lack of ginkgophytes, is of probable Neocomian rather than Aptian age as suggested by Dettmann et al. (1992).

A Neocomian–Barremian age is proposed for the collective Western Australian terrestrial plant assemblages described here. Accumulation of plant remains in several regions along the continent's western margin during the Neocomian–Barremian probably occurred as part of a single phase of widespread fluvio–deltaic sedimentation associated with continental breakup, marginal basin sag, and regional and global sea-level fluctuations at that time (McLoughlin, et al. 1994).

Comparisons with other Gondwanan floras

The Western Australian Cretaceous floras share several genera and possibly some species with the Rajmahal, Kutch, and Jabalpur floras of India. The Rajmahal Series has been variously assigned to: the lower, middle, or upper Jurassic according to traditional palaeobotanical studies (Feistmantel 1877a; Halle 1913; Sahni and Rao 1933); the Lower Cretaceous based on palynostratigraphy (Playford and Cornelius 1967); and the Albian according to radiometric (K-Ar) dating (McDougall and McElhinny 1970). Sukh-Dev (1987) re-evaluated the stratigraphic relationships of the Indian Mesozoic macrofloras and established 12 assemblage zones from the Early Triassic to latest Cretaceous. He reassigned the lower Rajmahal assemblages to the Cretaceous. Sukh-Dev's Lower (1987)Dictyozamites-Pterophyllum-Anomozamites Assemblage Zone corresponds most closely to the Western Australian Cretaceous floras by its high proportion of bennettitaleans, Taeniopteris, and the occurrence of comparable species of ferns

[Gleichenites (=Microphyllopteris), Hausmannia, and Cladophlebis] and Conifers [Arancaria, Arancarites (cone scales and cones), and Elatocladns]. This Indian zone differs from the Western Australian assemblages by its possession of ginkgophyte and Pachypteris species and its lack of Phyllopteroides, Roebuckia, and Nathorstianella species. The Dictyozamites-Pterophyllum-Anomozamites Assemblage Zone is best represented in the Jabalpur Formation (Chaugan Forest district) of Madhya Pradesh (Crookshank 1936), the Lower Rajmahal Formation (intertrappean beds 1-3, Rajmahal Hills) of Bihar (Bose and Sah 1968; Sharma 1969b, 1971, 1975; Zeba-Bano et al. 1979), and the lower Bhuj Formation of Kutch (Bose and Banerji 1984) together with a number of lesserstudied units in peninsula India, Sri Lanka, and Nepal (see Sukh-Dev 1987). Certain genera (and perhaps species) from Sukh-Dev's (1987) succeeding Allocladus-Brachyphyllum-Pagiophyllum Assemblage Zone and Weichselia-Onychiopsis-Gleichenia Assemblage Zone are also shared with the Western Australian floras but these assemblages appear to be more akin to the Victorian Zone C (?late Neocomian-early Albian) floras.

The Tico (Baqueró Formation) Flora of Patagonia (Argentina) has a number of conifer, fern, and bennettitalean genera in common with the Western Australian Cretaceous floras (Herbst 1962a; Archangelsky 1963a,b,c, 1964a,b; Archangelsky and Baldoni 1972) but the number of shared taxa are fewer than between the Western Australian and Indian assemblages. The Baqueró Formation has been assigned a late Barremian to early Aptian age based on its palynoflora (Archangelsky et al. 1984) and most notably differs from the Western Australian Early Cretaceous assemblages by its possession of angiosperm remains (Archangelsky 1963c; Romerro and Archangelsky 1986). It probably has greater floristic affinities with the Victorian Zone C assemblages.

A number of other lesser-studied Early Cretaceous floras from Argentina show distinct similarities to the Western Australian assemblages. Though dated as Aptian on the basis of associated ammonoid faunas, the Kachaike Formation, Santa Cruz, has yielded Microphyllopteris, Hausmannia, Cladophlebis, and Ptilophyllum species strikingly similar to those from the Broome Sandstone (Longobucco et al. 1985). The Apeleg Formation, Chubut, also contains species of Taeniopteris, Cladophlebis, and Ptilophyllum similar to those from Western Australia and has been assigned a Hauterivian-Barremian age (Baldoni and de Vera 1980). Although some elements (e.g., Ticoa, Zamites, and Cycadolepis spp.) differ, the Spring Hill Formation of southern Argentina and Chile also has a number of bennettitaleans, ferns, and

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conifers, which are comparable to Western Australian taxa, and has been assigned an Early Cretaceous (probable Hauterivian–Barremian) age (Archangelsky 1976; Baldoni 1979, 1980c; Baldoni and Taylor 1983).

Macrofloras from the South African Kirkwood, Mngazana, and Makatini Formations range from Berriasian to late Aptian in age and are represented by Marchantites, Ricciopsis, Cladophlebis, Sphenopteris, Onychiopsis, Taeniopteris, Pseudoctenis, Zamites, Dictyozamites, Araucaria, and Podocarpus species (Anderson and Anderson 1985). Most of these are readily distinguishable from Australian forms, a few are shared with South American assemblages but the majority appear to be endemic to South Africa suggesting an early floristic separation of this province from other Gondwanan regions.

The upper Fossil Bluff Formation flora (Barremian-Albian) of Alexander Island, Antarctica, contains Hausmannia, Cladophlebis, Taeniopteris, and Elatocladus species comparable to those in the Western Australian assemblages but differs in its possession of ginkgophytes, Pagiophyllum, Bellarinea, and Phlebopteris. The upper Fossil Bluff Formation floras correspond more closely with the Victorian Zone C assemblages. The Hope and Botany Bay floras of the Antarctic Peninsula were originally regarded as Jurassic in age (Halle 1913). Later studies suggested an Early Cretaceous age (Francis 1986; Gee 1989) based on an abundance of sphenopterid, cladophleboid, taeniopterid, bennettitalean, and podocarpacean remains similar to other Gondwanan Early Cretaceous assemblages. However, these Antarctic assemblages are characterized by the presence of possible sagenopterid pteridosperms and Goeppertella favouring an Early Jurassic age (Rees 1993).

Comparisons with extra-Gondwanan floras

Many plant families have wide, often cosmopolitan, distributions in the Jurassic, however, by Early Cretaceous times fragmentation of Pangaea led to renewed floral provincialism equivalent to that of the late Palaeozoic (Meyen 1987). Although some families and genera maintained wide distributions in the Early Cretaceous, Gondwanan floras are readily distinguishable from those of other provinces at species (and often genus) level. Geographically, the closest extra-Gondwanan landmasses to Australia during the Early Cretaceous were probably the series of disjunct terranes presently constituting South China, Indochina, and Malesia (Audley-Charles 1988; Metcalfe 1991). Although Mesozoic floras have been reported from these areas (Kimura and Ohana 1992), many have not yet been fully documented. Late Jurassic and Early Cretaceous floras of Japan are distinguished from Australian floras by the presence of, or greater representation of, bennettitalean taxa such as Zamites, Neozamites, Anomozamites, Dictyozamites, Ctenozamites, cycadaleans (such as Ctenis), czekanowskialeans, conifers and including Podozamites. Cupressinocladus, and Frenelopsis (Kimura and Ohana 1987a,b,c, 1992, 1988, 1989; Kimura et al. 1985, 1991, 1992). Malayan and Thai mid- to late Mesozoic floras (Kon'no 1967, 1972; Smiley 1970; Kon'no and Asama 1975; Asama et al. 1981) and coeval Indochinese macrofloras (Serra 1963, 1966; Vozenin-Serra 1977) have affinities with other southern (Ryoseki-type) east Asian floras (Kimura 1987, 1988) and have few if any elements in common with Australian assemblages.

Palaeoenvironments and palaeoclimates

The presence of high latitude forests and terrestrial vertebrate populations together with oxygen isotope signatures from marine invertebrates suggest globally raised temperatures during the Early and mid-Cretaceous (Frakes 1979: Douglas and Williams 1982; Barron 1983; Spicer and Parish 1986; Rich and Rich 1989; Frakes and Francis 1990). Various factors including reduced obliquity of the Earth's rotational axis, palaeogeographic configurations of continents and ocean currents, higher atmospheric CO, levels, and increased levels of solar radiation have been suggested as possible causes for the apparently high palaeotemperatures (Douglas and Williams 1982; Creber and Chaloner 1985; Barron 1983. 1984). Palaeomagnetic evidence (Veevers et al. 1991) indicates that the Early Cretaceous Western Australian floras existed in middle latitudes (45°-55°) within presumably warmer climates than those experienced by the higher palaeolatitude Victorian and Antarctic floras (Douglas 1969, 1973; Jefferson 1983). However, fossil woods from the Birdrong Sandstone show well-defined growth rings consistent with a distinctly seasonal climate. Analysis of 48 permineralized conifer wood samples from the Giralia Anticline, Carnarvon Basin (McLoughlin et al. 1994), showed mean sensitivity values in the range of 0.148 to 0.673 [i.e. complacent to strongly sensitive (Fritts 1976)] with an average mean sensitivity of 0.348 (moderately sensitive). These growth indices together with the presence of sporadic false growth rings within the woods suggest a pronounced seasonal climate but with substantial inter-seasonal variability in environmental parameters.

The presence of matted *Taeniopteris daintreei* leaves in the Bullsbrook Formation suggests a deciduous or semi-deciduous habit for these pentoxylaleans consistent with evidence from the Victorian Cretaceous (Douglas and Williams 1982; Drinnan and Chambers 1986) which suggests that

these plants were adapted to a seasonal climatic regime. A deciduous habit for other plant groups in the Western Australian assemblages is less obvious although the complete and sometimes matted fronds of bennettitaleans such as *Ptilophyllum cutchense* in the Broome Sandstone may reflect deciduousness.

The range of fern and lycophyte species in the collections suggests a humid microthermal to megathermal climate based on the distributions of related extant taxa. However, most of the fossiliferous units were deposited in lowland deltaic environments where high water table (rheotrophic) rather than necessarily high rainfall (ombotrophic) conditions may have aided the growth of pteridophytes. Modern cycadophytes typically grow in mesothermal to megathermal conditions and most forms probably occupied similar climates in the past (Douglas and Williams 1982). The abundance of bennettitalean foliage in the studied assemblages favours interpretation of a relatively warm (though seasonal) climate. Some of the bennettitaleans have comparatively small fronds (e.g., Ptilophyllum boolensis) which may have been a foliar response to local water stress.

Differential representation of plant groups between the various Western Australian Neocomian-Barremian assemblages is relatively minor and probably reflects local differences between depositional settings (e.g., alluvial valley versus coastal environments). The Nanutarra Formation yields a small macroflora mixed with a marine invertebrate fauna (Cox 1961) and was probably deposited within paralic to shallow marine conditions. The coastal to nearshore sediments of the Birdrong Sandstone lack leaf remains but contain abundant mollusc-bored fossil wood, ammonoids, and marine vertebrates (McLoughlin et al. 1994). Whilst some of the plant remains in the Broome Sandstone are clearly allochthonous, autochthonous root beds and Nathorstianella corms are evident in exposures at Gantheaume Point, Broome. This coarse-grained unit also contains diverse dinosaurian trackways (Long 1990) and sparse bivalves (Yeates et al. 1984) and was probably deposited within a deltaic setting. The plant-bearing Callawa Formation and Cronin Sandstone, although not examined during this study, lack invertebrate fossils and were probably deposited within proximal fluvial (alluvial valley/ alluvial plain) settings. The Leederville Formation consists of interbedded sandstones, siltstones, and claystones and was deposited within paralic to shallow marine environments (Cockbain 1990). The correlative Bullsbrook Formation is dominantly composed of sandstone but contains local plant-bearing overbank shale lenses and was deposited within fluvial environments (Cockbain 1990).

CONCLUSIONS

Thirty-two fossil plant and fungi taxa have been described from five Early Cretaceous lithostratigraphic units in Western Australia. Four new species (viz., Phyllopteroides westralensis, Roebuckia spatulata, Elatocladus ginginensis, and Carpolithes bullsbrookensis) are defined while several others are described under open nomenclature owing to insufficient or inadequately preserved material prohibiting comparisons to established taxa. The fossil assemblages comprise lycophytes, ferns. pteridosperms, pentoxylaleans, bennettitaleans, and araucarian and podocarpacean conifers. Bennettitaleans, pentoxylaleans, and conifers are the numerically dominant elements of the flora. Macrofossil suites from the Broome Sandstone (Canning Basin), Nanutarra Formation and Birdrong Sandstone (Carnarvon Basin), and Leederville and Bullsbrook Formations (Perth Basin) are correlated with Douglas' (1969) Ptilophyllum-Pachypteris austropapillosa Zone (Zone B) of Victoria and indicate a Neocomian-Barremian age. The Nanutarra Formation is a diachronous marginal marine to paralic unit and its age may locally extend to the Aptian based on invertebrate assemblages (Cox 1961). The Western Australian Early Cretaceous floras are most closely comparable with coeval assemblages from South Australia and the Northern Territory. Lesser similarities are evident with eastern Australian and Indian floras and fewer species are shared with South America, Antarctica, and South Africa. Few, if any, species are shared with extra-Gondwanan assemblages. The representation of plant groups, together with wood growth indices, palaeomagnetic data, and oxygen isotope signatures, suggests that the Western Australian marginal basins experienced humid seasonal mesothermal climates in mid-latitudes during the Neocomian-Barremian. Local variations between assemblages are probably attributable to differences in depositional settings, seasonal effects, and taphonomic factors rather than significant climatic or stratigraphic anomalies between localities and host formations.

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